The CANADIAN FIELD-NATURALIST

Published by THE OTTAWA FIELD-NATURALISTS' CLUB, Ottawa, Canada

Volume 128, Number 1

January–March 2014

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The Canadian Field-Naturalist

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COVER: Melanistic Maritime Gartersnake, *Thamnophis sirtalis pallidulus*, from Big Tancook Island, Mahone Bay, Lunenburg County, Nova Scotia, captured on 7 May 2012. Photographed after it shed its skin in the laboratory. Photo: R. Lloyd. See pages 63–71 in this issue.

THE CANADIAN FIELD-NATURALIST

Volume 128

2014

Volume 128
The Ottawa Field-Naturalists' Club Transactions

Promoting the study and conservation
of northern biodiversity since 1880

THE OTTAWA FIELD-NATURALISTS' CLUB

OTTAWA CANADA

The Canadian Field-Naturalist

Volume 128, Number 1 January–March 2014

Distribution and Abundance of Benthic Macroinvertebrates and Zooplankton in Lakes in Kejimkujik National Park and National Historic Site of Canada, Nova Scotia

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Nussbaumer, Christina, Neil M. Burgess, and Russ C. Weeber. 2014. Distribution and abundance of benthic macroinvertebrates and zooplankton in lakes in Kejimkujik National Park and National Historic Site of Canada, Nova Scotia. Canadian Field-Naturalist 128(1): 1–24.

As part of the Acid Rain Biomonitoring Program at Environment Canada, we sampled aquatic biodiversity in 20 acidic lakes in 2009 and 2010 in Kejimkujik National Park and National Historic Site of Canada and vicinity in Nova Scotia. We established an inventory of current aquatic macroinvertebrate and zooplankton species composition and abundance in each of the 20 study lakes. A total of 197 macroinvertebrate taxa were identified; the number of taxa observed was positively correlated with pH across the 20 lakes. Acid-tolerant taxa, such as isopods, amphipods, trichopterans, and oligochaetes, were common and abundant, while bivalves, gastropods, and leeches were lower in abundance. The number of isopods and amphipods collected was correlated with calcium concentration; a greater proportion of isopods than amphipods were collected from lakes with low calcium and low pH. Taxa with hard, calcareous shells, such as bivalves and gastropods, were not present in lakes with low calcium and low pH, with bivalves occurring only in lakes above pH 4.9. Odonates and ephemeropterans, which were low in abundance, were associated with a wide range of acidity. Coleopteran abundance was positively correlated with concentrations of dissolved organic carbon. A total of 26 zooplankton taxa were collected, but only cyclopoid abundance was correlated with lake pH. Results presented here provide a summary of aquatic biodiversity in lakes in Kejimkujik National Park and National Historic Site and vicinity and provide a baseline for future monitoring as acid deposition continues to affect this acid-sensitive region in Atlantic Canada.

Key Words: macroinvertebrates; Kejimkujik National Park and National Historic Site of Canada; water chemistry; acidic lakes; zooplankton; Nova Scotia

Introduction

Acid deposition remains a widespread stressor of freshwater ecosystems across southeastern Canada despite legislated reductions in emissions of acidifying pollutants over recent decades in both Canada and the United States (Jeffries *et al.* 2004; Ginn *et al.* 2007). Analyses of critical loads of acid deposition in eastern Canada have suggested regions with carbonate-poor geology continue to be influenced by acid inputs into the environment (Doka *et al.* 2003; Jeffries *et al.* 2003; Dupont *et al.* 2005; Clair *et al.* 2007, 2011). The effects of acidification on the diversity of aquatic macroinvertebrate species have been well studied (e.g., Dermott 1985; Peterson 1987; Schell and Kerekes 1989; Lento *et al.* 2008), and changes in the composition of the aquatic food web can have an impact on higher trophic levels that rely on these groups for food (Weeber *et al.* 2004).

In the 1980s, Environment Canada implemented the Acid Rain Biomonitoring Program to study aquatic invertebrate species assemblages in acid-sensitive Boreal Shield lakes in Ontario (McNicol *et al.* 1995b; Jeffries *et al.* 2004). In 2009 and 2010, this biomonitoring program was expanded to include Kejimkujik National Park and National Historic Site of Canada, which has a long history of environmental and ecological monitoring (Kerekes 1975; Kerekes *et al.* 1994; Burgess and Hobson 2006; Wyn *et al.* 2010; Clair *et al.* 2011).

In the period from 2000 to 2007, the Kejimkujik region in southwestern Nova Scotia received an average of 8 kg · ha^{-1} · year^{-1} to 12 kg · ha^{-1} · year^{-1} of SO_4^{2-} deposition (wet and dry) (Clair *et al.* 2011). This level is relatively low compared to the rest of North America. However, the geology of Kejimkujik National Park and National Historic Site consists mainly of poorly weath-

erable bedrock that offers little buffering capacity, and this makes this ecosystem extremely sensitive to additional inputs of acid from the atmosphere (Clair *et al.* 2007). In addition, the landscape in Kejimkujik National Park and National Historic Site and the surrounding area is composed of naturally acidic habitats due to the prevalence of bog and fen wetlands. Therefore, even with further reductions in atmospheric acid deposition, recovery in these aquatic ecosystems is expected to be extremely slow (Whitfield *et al.* 2006; Clair *et al.* 2011).

Although information on the status of and trends in lake chemistry in Kejimkujik National Park and National Historic Site is well developed (Clair *et al.* 2011), only limited research has been completed on the aquatic biodiversity in these acid-sensitive lakes (Kerekes and Freedman 1989; Schell and Kerekes 1989). The purpose of this study was: (i) to determine the current composition and abundance of aquatic invertebrate and zooplankton in 20 acid-sensitive lakes in Kejimkujik National Park and National Historic Site and vicinity and (ii) to identify potential indicator taxa with respect to biological responses to lake acidity.

Study Area

Kejimkujik National Park and Historic Site is a protected area of 404 km^2 located in southwestern Nova Scotia (Figure 1). Twenty study lakes (17 within the Park and 3 in the vicinity) were selected to cover a range of water chemistry parameters. Lakes were chosen to cover the largest possible gradients of acidity/alkalinity, calcium, colour, and concentration of dissolved organic carbon in the study area. All of the 20 lakes were accessible by road or canoe (some backcountry lakes in Kejimkujik National Park and Historic Site are not accessible by road, so accessibility was also a factor). Eight of the lakes were sampled in

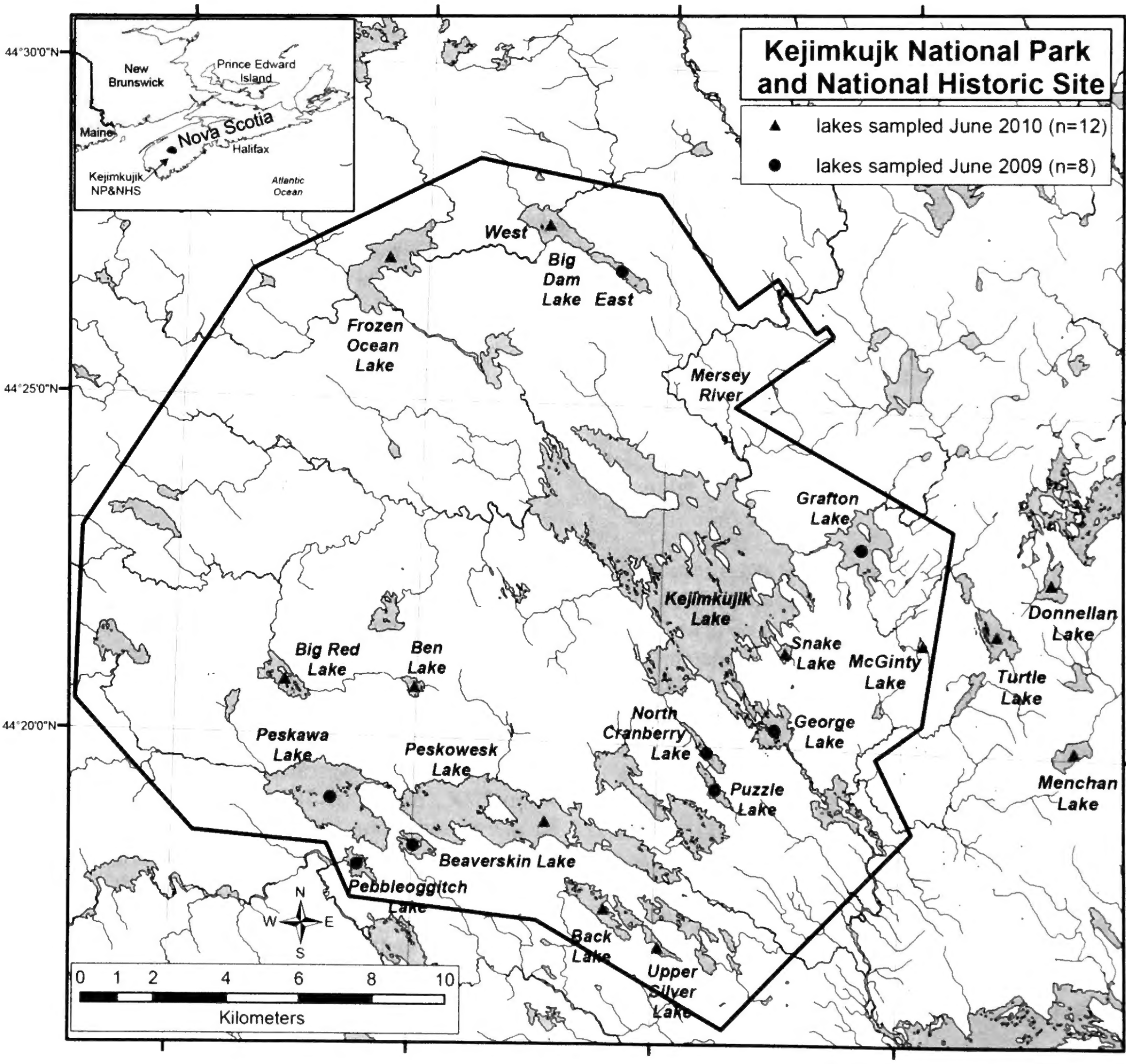

FIGURE 1. Location of 20 acid rain biomonitoring study lakes sampled during 2009 and 2010 in Kejimkujik National Park and National Historic Site of Canada and surrounding area, Nova Scotia.

June 2009 (Beaverskin, Big Dam East, George, Grafton, North Cranberry, Pebbleloggitch, Peskawa, and Puzzle) and the remaining 12 lakes were sampled in June 2010 (Back, Ben, Big Dam West, Big Red, Donnellan, Frozen Ocean, Menchan, McGinty, Peskowesk, Snake, Turtle, and Upper Silver).

Methods

Sampling methods

As part of an Environment Canada lake monitoring network, surface water samples were collected by helicopter from the centre of each lake during the spring and fall turnover periods each year (usually May and October) (Clair *et al.* 2011). Samples were collected at a depth of 0.5 m, kept cool, and shipped overnight to the Environment Canada Atlantic Laboratory for Environmental Testing (ALET) in Moncton, New Brunswick. At every 10th lake, triplicate samples were collected and compared to each other for quality control. All water samples were analyzed in the laboratory for various water chemistry parameters using unfiltered water following ALET protocols (Clair *et al.* 2011; Eaton *et al.* 2012).

For the collection of aquatic macroinvertebrates and zooplankton, we followed the sampling protocols of the Environment Canada Acid Rain Biomonitoring Program in Ontario and Quebec (see McNicol *et al.* 1995b). Sampling was completed in mid-June, as this is a time of high invertebrate biomass and richness and it is also when local waterbirds that depend on aquatic prey to raise their young are breeding (McNicol *et al.* 1996).

At each study lake we conducted 10 benthic drag samples, 10 water column sweeps, and 10 hoop samples, and we set 6 minnow traps (McNicol *et al.* 1996). All samples were taken at randomly selected sites. Benthic drag samples, which targeted odonates, ephemeropterans, bivalves, and gastropods, were conducted in water less than 1 m in depth. A D-frame dip net (0.85 mm mesh) was dragged over the substrate for a distance of 0.5 m to collect the top 1–2 cm of substrate (total sample area of 0.14 m^2) (McNicol *et al.* 1996). If boulders or rocky substrates made benthic drag sampling impractical, a traveling kick and sweep sample was completed instead. For these samples, the sampler walked backwards for a distance of 1 m along the shoreline (maximum 1 m depth), kicking the bottom substrate and sweeping the dislodged detritus and invertebrates into the D-frame net (Rosenberg *et al.* 2000).

Both the benthic drag and the travelling kick and sweep samples were processed in the same way: detritus in the net was thoroughly rinsed to remove fine sediments and was transferred to a sample container, where it was first preserved with 10% buffered formalin for 48 hours and then transferred into 70% ethanol. Entire benthic samples were later sorted under a dissecting microscope. All observed macroinvertebrates were removed and preserved in 70% ethanol.

Sweep sampling targeted nektonic invertebrates active in the water column. Sweep sampling was conducted in open water less than 5 m from the shore. Sampling was completed by sweeping through the water column in 10 consecutive arcs using a D-frame dip net (0.85 mm mesh, 625 cm^2 capture area) over the bow of a forward-moving canoe traveling parallel to the shoreline. Each sweep described an arc from the water surface down to a maximum depth of 1 m and back to the surface, and a new section of the water column was sampled with each arc. Captured invertebrates were picked from the net using forceps and transferred to a sample container containing 70% ethanol.

Hoop sampling targeted trichopterans and gastropods. A circular hoop of coated wire (diameter of 0.64 m, area of 0.32 m^2) was placed on the substrate in water <0.5 m deep. The hoop was visually searched for a total of 5 minutes, and all invertebrates observed on the surface of the substrate and vegetation were removed and preserved in 70% ethanol.

All benthic macroinvertebrates from hoops, sweeps, kick and sweep samples, and benthic drags were later identified to species (or lowest taxonomic level possible).

Minnow traps targeted large nektonic invertebrates. Six standard Gee's minnow traps were baited with dry dog food (Purina Puppy Chow®) and set for a total of 24 hours in near-shore sites where water depth was approximately 1 m. Specimens were preserved in 70% ethanol.

Zooplankton sampling was conducted at 15 of the 20 study lakes (5 of the study lakes were $\leq$2 m deep and were therefore too shallow for vertical zooplankton sampling to be carried out). A single vertical haul was completed at the deepest part of each lake, starting from 1 m above the sediment to the water's surface. Samples were collected using a non-metered zooplankton net (80 μm mesh, 26 cm in diameter). The contents of the net were rinsed into the bottom of the collection jar and then poured into a sample jar containing 33% sugared, buffered formalin. All zooplankton samples were identified to species (or lowest possible taxonomic level).

Data analysis

Counts from all benthic invertebrate sampling procedures were pooled within each lake for the statistical analyses. The resulting data from the 20 study lakes were summarized with respect to mean, minimum, and maximum counts for each species, as well as the percentage of lakes where a given species was observed. Rare species (n = 72 taxa) were defined as occurring in $\leq$ 10% of the study lakes, while common species (n = 125 taxa) occurred in > 10% of the study lakes. The abundance and percentage composition of the most abundant taxonomic groups were determined for each lake, and boxplots where generated to show trends for individual taxonomic groups of interest. Taxonomic richness was calculated as the total number of unique taxa in each lake.

Associations between water chemistry parameters, as well as between the total number of macroinvertebrate taxonomic groups and lake acidity, were evaluated using Spearman rank correlations. This non-parametric method of statistical analysis was employed as some of the data did not meet assumptions of normality required for Pearson's correlations. All statistical analyses were completed using SYSTAT 13 (SYSTAT Software Inc., Chicago, Illinois).

Zooplankton data were summarized by mean density (number of individuals/m^3) for each of the 15 lakes, and the percentage of lakes a given species was observed in was also calculated.

Results

Fish were present in all 20 of the study lakes (Kerekes 1975; Drysdale *et al.* 2005). Mean water chemistry values for each lake are presented in Table 1. Many of the study lakes were oligotrophic and darkly coloured (99–202 Hazen units) due to dissolved organic compounds leached from nearby bogs. Mean lake pH varied from 4.3 (Big Red Lake) to 6.6 (McGinty Lake) (Table 1). pH and calcium concentrations were positively correlated in the study lakes ($r_s = 0.747$, $P < 0.001$); pH and dissolved organic carbon were negatively correlated ($r_s = -0.715$, $P < 0.001$).

A total of 26 zooplankton species were observed in the study lakes, with many of the common taxa observed across a wide gradient of acidity (Supplementary Table 1). Only the abundance of Cyclopoida was significantly correlated with lake pH ($r_s = 0.536$, $P = 0.040$).

A total of 197 taxa of aquatic macroinvertebrates were observed (149 were identified to species, 38 to genus, and 10 to family) (Supplementary Table 2). The total number of taxa in each lake was positively correlated with both lake pH (Figure 2) ($r_s = 0.554$, $P = 0.011$) and calcium concentrations ($r_s = 0.463$, $P = 0.040$). Taxon richness was not significantly associated with dissolved organic carbon ($r_s = -0.390$, $P = 0.090$). Total abundance (number of individuals of all macroinvertebrates captured in each lake) was not correlated with any water chemistry parameter.

The most abundant benthic invertebrate groups in the 20 study lakes were Isopoda, Amphipoda, Oligochaeta, and Trichoptera (Figures 3A and 3B). Only one species of isopod was observed (*Caecidotea communis*), but it constituted up to 60% of the macroinvertebrates collected in some lakes (e.g., Peskowesk Lake) (Figure 3A). The abundance of isopods (*Caecidotea communis*) was lower in lakes with high pH and calcium levels and higher in lakes with low calcium levels (Figure 4A) ($r_s = -0.614$, $P = 0.004$). Amphipods were also abundant, with *Hyalella azteca* collected in 19 of the 20 lakes. There was a significant positive relationship between amphipod abundance and calcium levels (Figure 4B) ($r_s = 0.776$, $P < 0.001$). The proportion of isopods relative to amphipods decreased with increasing lake pH and calcium, with two exceptions (Big Dam East Lake and Turtle Lake) (Figure 4C).

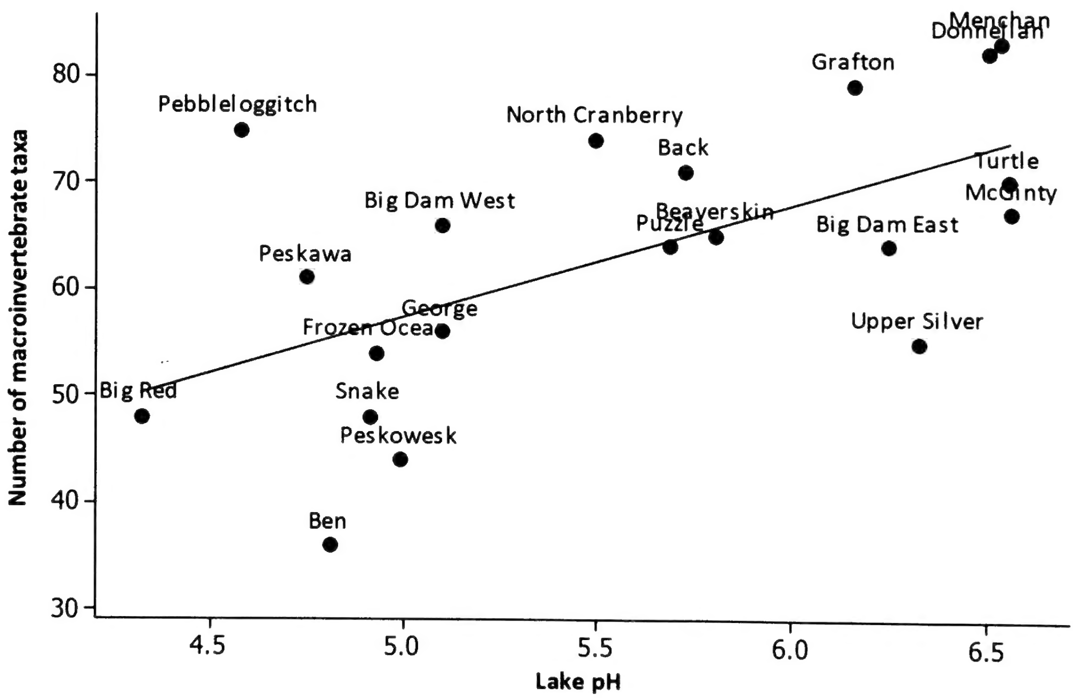

FIGURE 2. Total number of aquatic invertebrate taxa observed in relation to pH of 20 lakes sampled in June 2009 and 2010 in Kejimkujik National Park and National Historic Site of Canada and vicinity in Nova Scotia. Note the significant positive trend between lake pH and the number of invertebrate taxa ($P = 0.005$, $r_s = 0.36$).

TABLE 1. Mean water chemistry parameters for 20 lakes sampled in 2009 and 2010 in Kejimkujik National Park and National Historic Site of Canada, Nova Scotia, arranged from lowest to highest pH. Water samples were collected during spring and fall turnover in 2009 and 2010 as part of Environment Canada's acid rain monitoring program in Atlantic Canada (Clair *et al.* 2011).

Lake	pH	Alkalinity (mg/L $CaCO_3$)	SO_4 (mg/L)	Dissolved organic carbon (mg/L)	Nitrogen (N) (mg/L)	Calcium (Ca) (mg/L)	Magnesium (Mg) (mg/L)	Sodium (Na) (mg/L)	Chlorine (Cl) (mg/L)	Potassium (K) (mg/L)	Iron (Fe) (mg/L)	Aluminum (Al) (mg/L)	Colour (Hazen units)	Area (ha)	Mean depth (m)	Maximum depth (m)	Elevation (m)
Big Red	4.3	<0.01	1.07	19.53	0.38	0.28	0.33	2.80	3.58	0.26	0.20	0.30	202	70.5	1.0	2.2	160
Pebbleloggitch	4.6	<0.01	1.04	13.70	0.31	0.28	0.28	2.66	3.38	0.22	0.22	0.30	150	33.4	1.4	2.5	120
Peskawa	4.8	<0.01	1.30	9.83	0.28	0.29	0.26	2.63	3.69	0.27	0.18	0.30	99	388.5	3.2	9.0	120
Ben	4.8	0.05	1.29	6.23	0.21	0.18	0.23	2.43	3.52	0.34	0.10	0.15	56	20.4	0.5	0.7	170
Snake	4.9	0.41	0.53	14.73	0.40	0.66	0.41	2.74	3.86	0.16	0.43	0.13	159	12.7	1.4	2.5	90
Frozen Ocean	4.9	0.34	1.06	13.28	0.32	0.62	0.38	3.30	4.36	0.32	0.27	0.29	128	228.0	1.9	7.6	105
Peskowesk	5.0	0.45	1.38	6.90	0.22	0.30	0.28	2.71	3.88	0.25	0.17	0.25	69	685.0	3.9	13.0	105
Big Dam West	5.1	0.58	1.08	12.63	0.31	0.73	0.39	3.72	5.09	0.30	0.26	0.27	114	105.0	2.5	9.5	120
George	5.1	0.67	1.37	9.63	0.26	0.58	0.36	3.20	4.47	0.29	0.27	0.21	100	108.0	2.4	8.5	87
North Cranberry	5.5	0.54	1.29	4.33	0.21	0.38	0.29	2.53	3.68	0.23	0.07	0.08	29	38.0	1.5	5.0	105
Puzzle	5.7	0.79	1.10	3.60	0.16	0.38	0.28	2.42	3.63	0.28	0.07	0.05	13	36.0	2.7	6.1	120
Back	5.7	0.66	1.49	4.13	0.20	0.46	0.32	2.62	3.89	0.22	0.06	0.08	28	64.9	2.2	5.8	100
Beaverskin	5.8	0.56	1.41	2.83	0.18	0.29	0.30	2.61	3.86	0.24	0.02	0.04	11	39.5	2.2	6.3	120
Grafton	6.2	1.55	1.59	6.43	0.25	0.94	0.49	4.36	6.34	0.23	0.28	0.09	52	270.4	2.8	10.0	100
Big Dam East	6.2	1.34	1.38	4.45	0.21	0.61	0.38	3.09	4.25	0.27	0.05	0.09	24	45.5	2.3	4.2	120
Upper Silver	6.3	1.38	1.49	3.60	0.17	0.64	0.33	2.77	3.86	0.25	0.03	0.07	18	24.3	2.3	5.8	90
Donnellan	6.5	2.19	1.61	4.00	0.19	0.86	0.47	4.44	6.48	0.39	0.08	0.06	25	47.6	–	–	110
Menchan	6.5	2.32	1.82	2.90	0.16	0.74	0.46	2.65	3.47	0.38	0.04	0.03	13	51.1	6.5	12.0	126
Turtle	6.6	2.49	1.57	3.90	0.17	0.98	0.48	2.78	3.93	0.41	0.08	0.06	24	85.2	4.5	9.0	103
McGinty	6.6	3.11	0.97	7.70	0.32	1.12	0.51	2.70	3.69	0.27	0.37	0.08	61	4.4	1.4	4.0	105

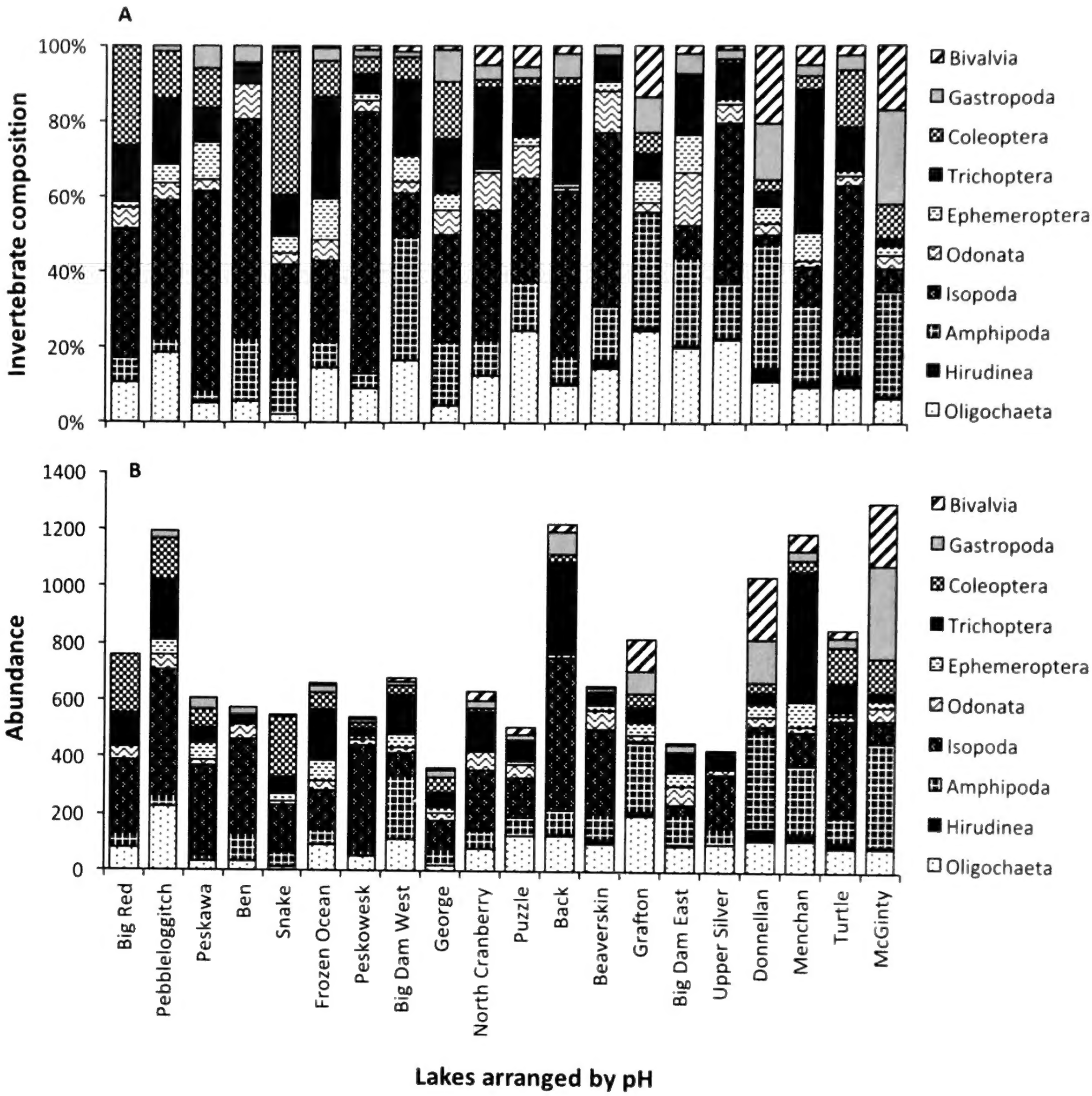

FIGURE 3. Percentage composition (panel A) and total abundance (panel B) of various taxonomic groups sampled in June 2009 and 2010 in 20 lakes in Kejimkujik National Park and National Historic Site of Canada and vicinity in Nova Scotia. Total abundance is the total number of individuals collected per lake. Lakes are arranged from the most acidic (Big Red Lake) (pH 4.3) to the least acidic (McGinty Lake) (pH 6.6).

Lakes with high pH and calcium concentrations had a larger number of bivalves, gastropods, and leeches (Hirudinea) (Figure 5). Bivalves were observed only in lakes with pH greater than approximately 4.9, and abundance was significantly correlated with lake acidity (Figure 5A) (r_s = 0.775, $P < 0.001$). Gastropod abundance was also significantly correlated with pH (Figure 5B) (r_s = 0.539, P = 0.014). Similarly, Hirudinea abundance was significantly correlated with lake pH (Figure 5C) (r_s = 0.789, $P < 0.001$). No leeches were collected from lakes with pH <5.5, with the exception of a few individuals from the Erpobdellidae family captured in Peskawa Lake (pH 4.8) and Peskowesk Lake (pH 5.0). In contrast, abundance of coleopterans was significantly correlated with dissolved organic carbon (Figure 6) (r_s = 0.650; P = 0.002), but not with pH or calcium ($P > 0.05$).

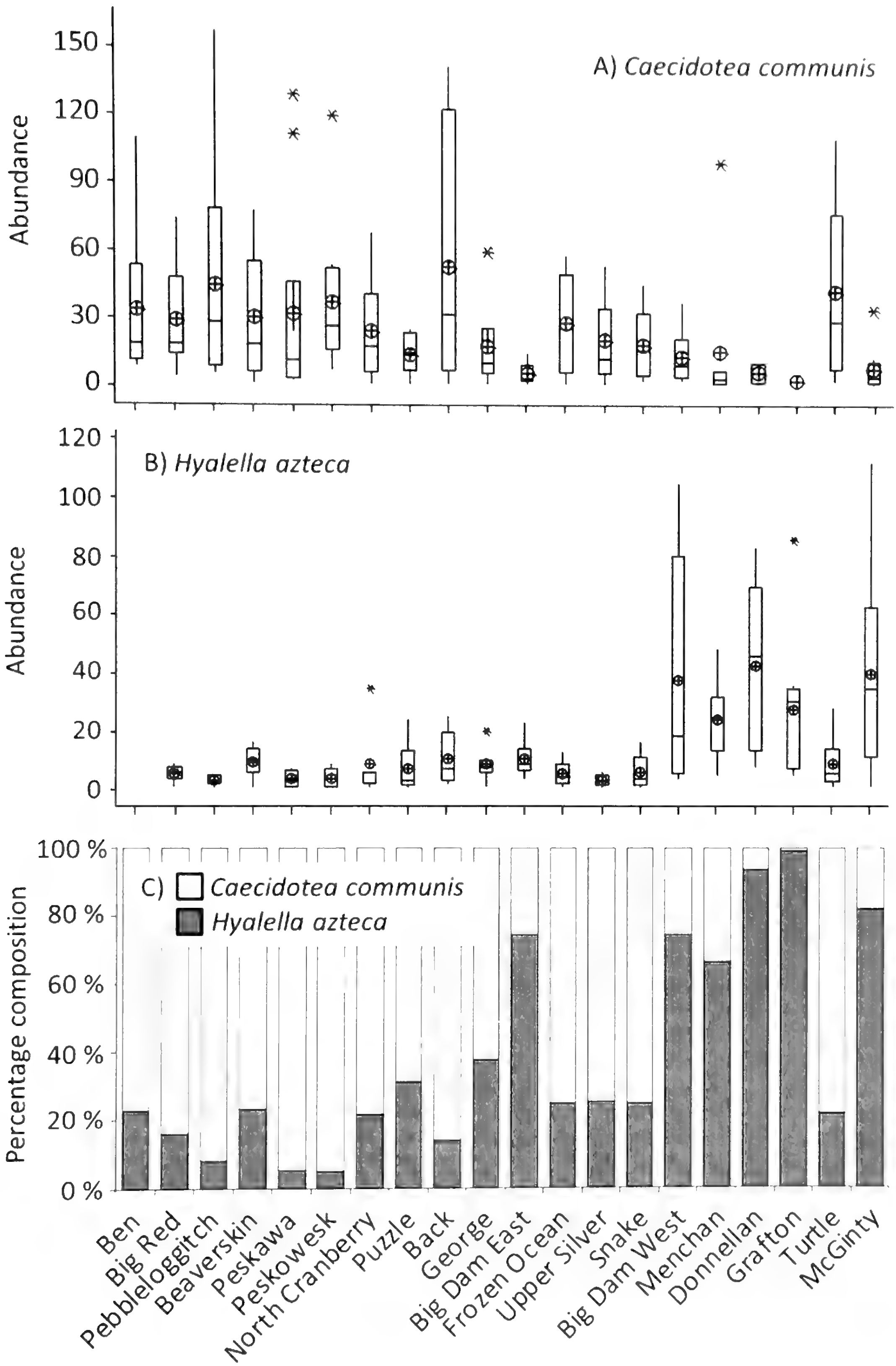

FIGURE 4. Abundance of the isopod *Caecidotea communis* (panel A), the amphipod *Hyalella azteca* (panel B), and the corresponding proportions of these two species (panel C) observed in 20 lakes sampled in June 2009 and 2010 in Kejimkujik National Park and National Historic Site of Canada and vicinity in Nova Scotia. Lakes are arranged by level of calcium from the lowest (Ben Lake) (0.18 mg/L) to the highest (McGinty Lake) (1.12 mg/L). For panels A and B, the horizontal line indicates the median, ⊕ indicates mean, box indicates 25th and 75th percentiles, whiskers indicate minimum and maximum data points within 1.5 × the box height from the bottom or top (respectively), and asterisks mark outliers.

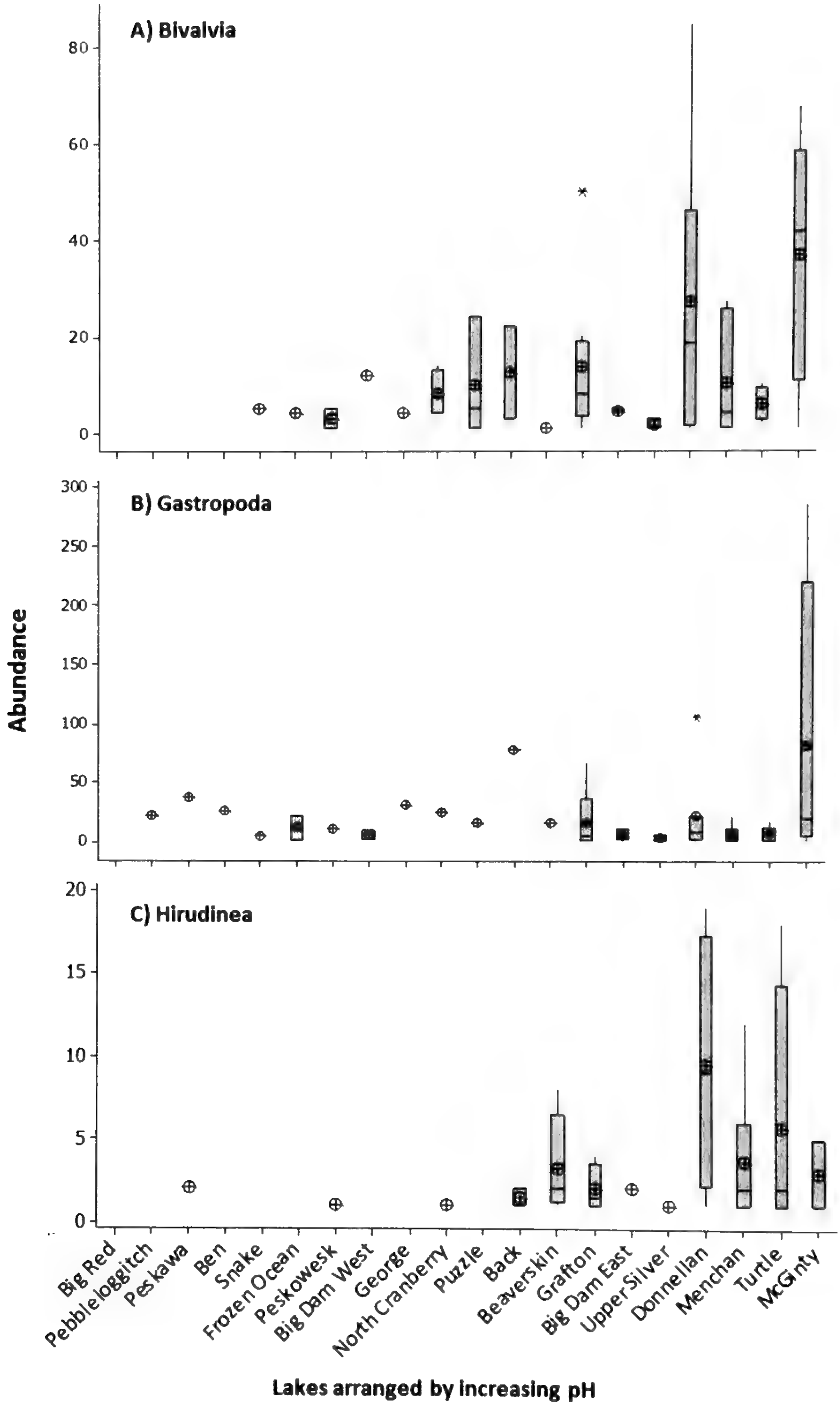

FIGURE 5. Abundance of Bivalvia (panel A), Gastropoda (panel B) and Hirudinea (leeches) (panel C) in 20 lakes sampled in June 2009 and 2010 in Kejimkujik National Park and National Historic Site of Canada and vicinity in Nova Scotia. Lakes are arranged from the most acidic (Big Red Lake) (pH 4.3) to the least acidic (McGinty Lake) (pH 6.6). Horizontal line indicates the median, ⊕ indicates mean, box indicates 25th and 75th percentiles, whiskers indicate minimum and maximum data points within 1.5 × the box height from the bottom or top (respectively), and asterisks mark outliers.

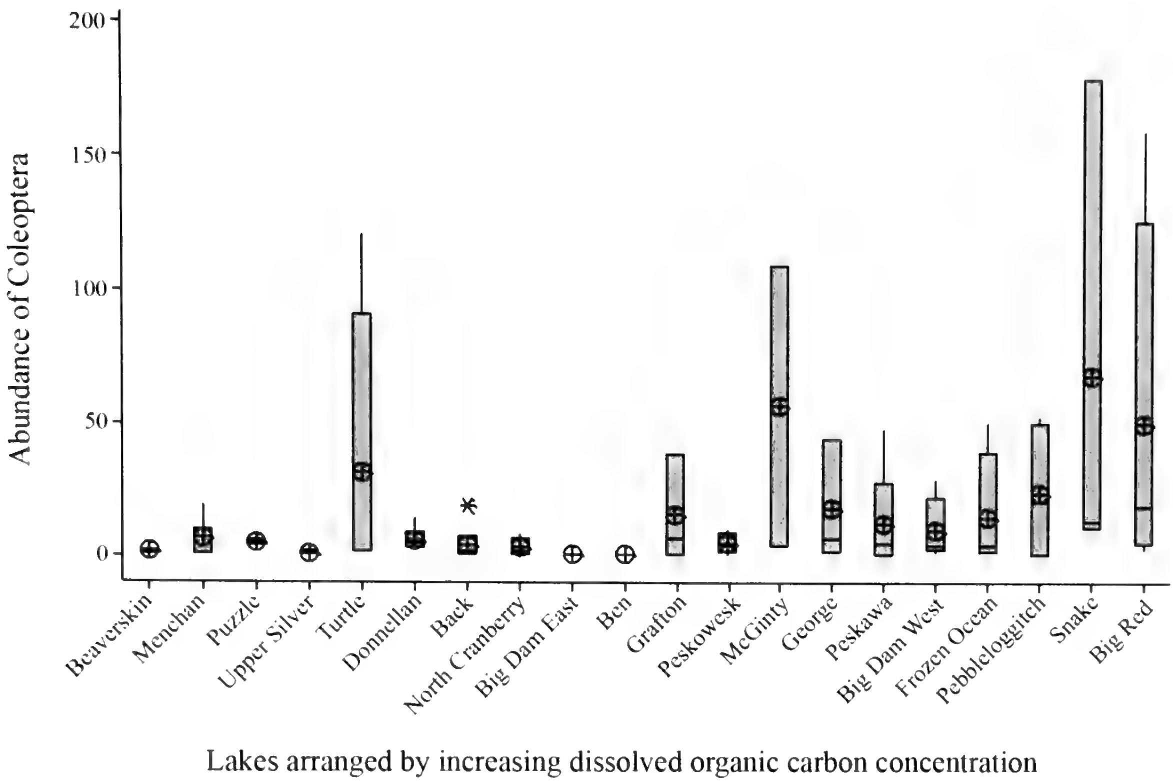

FIGURE 6. Abundance of Coleoptera in 20 lakes sampled in June 2009 and 2010 in Kejimkujik National Park and National Historic Site of Canada and vicinity in Nova Scotia. Lakes are arranged by concentration of dissolved organic carbon from the lowest (Beaverskin Lake) (2.8mg/L) to the highest (Big Red Lake) (19.5mg/L). Horizontal line indicates the median, ⊕ indicates mean, box indicates 25th and 75th percentiles, whiskers indicate minimum and maximum data points within 1.5 × the box height from the bottom or top (respectively), and asterisks mark outliers.

Discussion

We found that both pH and calcium were significantly correlated with the number of aquatic macroinvertebrate taxa observed in the study lakes. Lakes that were less acidic and lakes with higher calcium concentrations tended to have greater species richness. These findings are consistent with other studies, which also reported fewer aquatic invertebrate taxa in more acidic lakes (McNicol *et al.* 1995a; Doka *et al.* 1997). However, the relationship between chemical conditions and the abundance of macroinvertebrates was less clear.

Fish were present in all of the study lakes (Kerekes 1975; Drysdale *et al.* 2005), and the presence of fish likely influenced the macroinvertebrate and zooplankton species richness. The most frequently collected taxa were isopods, amphipods, and trichopterans. Gastropods, bivalves, and ephemeropterans, commonly considered to be more sensitive to acidity, were collected less frequently during the study. Lakes with lower pH had fewer taxa (consisting mostly of isopods, coleopterans, and oligochaetes), while lakes with higher pH had greater taxa richness.

Isopoda and amphipoda

Only one species of isopod was collected (*Caecidotea communis*), but this species was present in all 20 study lakes. *Caecidotea communis* was also the most abundant taxon in many of the study lakes, comprising ≥ 30% of the macroinvertebrates collected in 11 of the lakes. The abundance of this species was negatively correlated with calcium concentrations, and the highest numbers were found in the most acidic lakes (e.g., Peskawa Lake, Ben Lake, Peskowesk Lake). Schell and Kerekes (1989) also reported Isopoda in Nova Scotia lakes with pH as low as 4.4.

Isopods are known to be acid tolerant (Merritt *et al.* 2008), but their high frequency of occurrence in lakes in this study contrasts with their relative rarity in lakes monitored in Ontario (RCW *et al.*, unpublished data). Potential explanations include differences in the species found in the two datasets (Ontario isopods were identified only to order), regional differences in species habitat affinities, or a relative dominance of substrate type or other habitat conditions that encourage isopod abundance in lakes in this study area. Because sampling methods were similar in the two regions, we do not believe sampling variation is likely to be responsible for these differences.

Amphipods were also common, and their abundance was greater in lakes with high pH and high calcium concentrations. Two species of amphipods were col-

lected: *Crangonyx richmondensis* (collected in 55% of study lakes) and *Hyalella azteca* (collected in 95% of study lakes). In this study, *H. azteca* was present across a broad pH range (i.e., 4.3 to 6.6). Studies in Ontario have identified this species as acid sensitive (McNicol *et al.* 1995a), with a minimum pH threshold of 5.6 or higher (Stephenson *et al.* 1986; Rosenberg *et al.* 1997; Snucins 2003). In this study, however, *H. azteca* appeared to be very acid tolerant and was observed in lakes with pH as low as 4.3.

Peterson (1987) also observed *Hyalella* in lakes with low pH (4.5–5.5) in Nova Scotia and New Brunswick, and reported that *Hyalella* species in lakes in the Maritimes appear to be more tolerant of acidic conditions than other Amphipoda. However, the lakes in that particular study had higher concentrations of calcium than the study lakes with low pH in southwestern Nova Scotia or in acidified lakes in Ontario (Peterson 1987). The lakes in this study with low pH also had low calcium concentrations.

It may be possible that a localized population of *H. azteca* has adapted to the acidic environment in the lakes in Kejimkujik National Park and National Historic Site. A genetic study by Witt and Hebert (2000) examined populations of *H. azteca* from various locations across North America and found a complex of at least seven species rather than a single species as previously believed. Grapentine and Rosenberg (1992) also suggested that populations of *H. azteca* may have adapted to acidic conditions in some regions of Canada.

Interpretation of regional variation in *H. azteca* habitat associations and identification of their potential role in biological monitoring of lakes in this study area would benefit from an improved understanding of the geographic variation in their genetic profile and the consequences for their tolerance of acidic conditions.

When we compared the relative proportions of isopods and amphipods across the 20 study lakes, we found that isopods were dominant in lakes with low pH and low calcium concentrations while amphipods were dominant in lakes with high pH and high calcium concentrations. Both amphipods and isopods are photosensitive and avoid bright light by moving into crevices or under rocks, leaves, and roots (Covich and Thorp 2001, page 791), where they are less exposed (complex substrates provide protection from predation by fish and crayfish) (Covich and Thorp 2001, page 791). The substrate in many of the study lakes consists of cobbles and boulders, which may partially explain the high abundance of these two taxa.

Bivalvia and gastropoda

Invertebrate taxa with hard, calcareous shells such as bivalves and gastropods were generally collected only from less acidic lakes. A total of 10 species of bivalves and 12 species of gastropods were collected. Bivalve abundance was correlated with lake pH: bivalves were observed only in lakes where pH was greater than 4.9. Because many lakes in the study area are acidic and have low calcium concentrations, low abundance of calcium-dependent macroinvertebrate taxa was expected. Our results are consistent with a previous study of 8 acid-sensitive Nova Scotia lakes by Schell and Kerekes (1989), which found that bivalves did not occur below a pH of 5.0.

This exclusion of calcareous species in acidic lakes has also been noted for other acid-sensitive regions of eastern Canada (Weeber *et al.* 2004; Jeziorski *et al.* 2008). As calcium concentrations in many acidified lakes continue to decline (Jeziorski *et al.* 2008), this may further reduce the abundance and distribution of calcium-rich taxa such as bivalves and gastropods in lakes in the study area.

Gastropods were also generally more abundant in lakes with high pH and high calcium concentrations; this finding is consistent with results from Ontario (Bendell and McNicol 1993). One exception to this is *Ferrissia fragilis*, which was the only species collected in lakes in the study area with pH lower than 6. Bendell and McNicol (1993) also reported *Ferrissia* as an acid-tolerant gastropod in study lakes in Ontario, where it was the only gastropod taxon observed in lakes with pH below 6. That study also suggested that, above the minimal pH thresholds, gastropod abundance in small oligotrophic lakes was not limited by acidity or calcium concentrations but rather by food resources. Predation, substrate type, and macrophyte biomass can also play a large role in gastropod distributions (Brown 2001, page 310). In our study lakes, the abundance of *Ferrissia fragilis* also did not appear to be associated with pH, calcium, or dissolved organic carbon and thus is likely limited by some other constraint such as predation or availability of food resources.

Hirudinea

A total of 12 species of leeches were collected from the study lakes, with only 4 of those species being common (i.e., occurring in >10% of the lakes). Counts were generally low, and abundance was correlated with lake pH. Hirudinea were not observed in lakes with pH < 5.5, with the exception of two *Mooreobdella fervida* collected in Peskawa Lake (pH 4.8) and one *Erpobdella punctata* collected in Peskowesk Lake (pH 5.0).

Bendell and McNicol (1991) observed similar reductions in the diversity and abundance of Hirudinea in acidic conditions below pH 5.5. However, they suggested that acidity alone does not predict the distribution of leech species and that predation and availability of suitable prey also influenced their distribution (Bendell and McNicol 1991). In addition, other studies have shown that, although leeches are sensitive to low pH, their occurrence and abundance are also influenced by other factors, such as lake productivity (Schalk *et al.* 2001). Lakes in Kejimkujik National Park and National Historic Site are oligotrophic and generally have low

productivity (especially at the lower pH range), and lower abundance of preferred prey may therefore play an important role in the distribution of leeches there.

Coleoptera

Although lower in abundance than other groups, coleopterans appeared to be tolerant of acidity and were collected in all 20 study lakes. A total of 14 taxa were observed (8 were common and 6 were uncommon). The abundance of this taxonomic group was correlated with dissolved organic carbon. A study of Ontario lakes by Lento *et al.* (2008) also suggested a strong correlation between macroinvertebrate abundances and dissolved organic carbon, especially in acidic lakes. Wood *et al.* (2011) reported that dissolved organic carbon can protect against the deleterious effects of low pH on organismal function via physiological mechanisms. Dissolved organic carbon can alter the permeability of cell membranes in acidic conditions and also influence transport physiology (Wood *et al.* 2011).

Other studies have suggested that water chemistry is not as important a stressor on coleopterans as predation by fish (Bendell and McNicol 1987; Arnott *et al.* 2006). The darkly coloured water of some lakes in the study area (due to high concentrations of dissolved organic carbon) may provide coleopteran taxa with some protection from predation by fish and other visual predators.

Trichoptera

Trichopterans were common and taxonomically diverse in the study lakes, with 23 of the 30 taxa occurring in >10% of the lakes. Trichopteran species collected included taxa from 10 families, with the most common and abundant families being Hydroptilidae, Leptoceridae, and Limnephilidae. The trichopterans collected in the study lakes generally had a high apparent tolerance to acidity, with many of the observed species occurring across a wide gradient in lake pH.

Trichoptera abundance can be strongly influenced by fish predation, and trichopterans generally associated with fishless conditions, such as the leptocerid *Triaenodes* and phryganeid *Banksiola* (Bendell and McNicol 1995), were rare in the study lakes. Both of these organisms are quite large and thus are likely to be attractive prey for insectivorous fish. In contrast, the leptocerid *Nectopsyche* was quite abundant. They are smaller in size and construct cases with bristling twigs or elongate sticks attached that may make them more difficult for fish to consume as prey (Wiggins 2004).

Ephemeroptera and odonata

Ephemeroptera generally had low abundance in the 20 study lakes, with a total of 10 taxa collected. This is likely due to the acidity of the lakes, as ephemeropterans are recognized as being sensitive to acidity (Carbone *et al.* 1998). Seven of the ephemeropteran taxa were common, and 3 were uncommon. The most frequently collected species were *Caenis diminuta* and the genus *Eurylophella*, which have been reported to have at least some tolerance to acidity (Carbone *et al.* 1998). No ephemeropterans were collected from Ben Lake, which is low in pH (4.8) and had the lowest calcium levels of the 20 study lakes (0.18mg/L).

Odonates were taxonomically diverse in the study lakes, with a total of 30 species observed (22 species were common and 8 were uncommon). However, counts were generally low, and odonates did not make up a large proportion of macroinvertebrates in terms of abundance. The most abundant family of damselflies (suborder Zygoptera) was Coenagrionidae, which was observed across a wide gradient of acidity. Larvae in this family are relatively small (Hilsenhoff 2001, page 671) and thus may be less visible to predators such as fish or larger predatory odonates.

Within the suborder Anisoptera (dragonflies), the most common families observed in the study lakes were Corduliidae, Gomphidae, and Libellulidae, while Aeshnidae were rare. Anisoperta taxa also occurred across a wide gradient of acidity; for example, *Cordulia shurtleffi* was observed in 65% of the study lakes (pH 4.3–6.6). Bendell and McNicol (1995) also found that abundance of this particular taxon was not related to lake acidity in Ontario lakes.

Diptera

With the exception of chironomids, Diptera were not abundant in the study lakes. Ceratopogonidae were present in all 20 study lakes, and no correlation with acidity was detected. Chironomidae were frequently collected in all of the study lakes, but were not targeted in our sampling and sorting, so specimens were not identified to species level.

Hemiptera

Very few water striders were captured in the study lakes. The only species with high abundance was *Rheumatobates rileyi*, in particular in Upper Silver Lake. Although the abundance of this particular species has been shown to have a strong correlation with pH (Bendell 1988), acidity did not appear to be the main driver in the presence of this particular species in the study lakes.

Zooplankton

Of the 26 zooplankton species observed in the 15 study lakes, many were common and occurred across a wide gradient of acidity. Daphniids were the only taxonomic group that showed a clear correlation with acidity in the study lakes: they were not observed below a pH of 5.5. This finding is consistent with previous studies, which have shown daphniids to be acid sensitive (Yan *et al.* 2008; Korosi and Smol 2012). In addition, daphniids are sensitive to calcium levels (Jeziorski *et al.* 2008), and this may also explain their absence in the lakes that had low pH and low calcium concentrations.

With the exception of daphniids, zooplankton abundance in the study lakes did not appear to be correlated with acidity alone. Dissolved organic carbon has been

shown to affect zooplankton populations, and the high concentrations of dissolved organic carbon in some of the study lakes may provide some protection from visual predators (Yan *et al.* 2008). Using paleolimnological methods in 3 lakes in Kejimkujik National Park and National Historic Site, Korosi and Smol (2012) found that there was a more pronounced change induced by acidification in the assemblage of cladocerans in clearwater lakes with lower concentrations of dissolved organic carbon over time than in assemblages in dark water lakes with more dissolved organic carbon. Zooplankton can also be influenced by a large variety of natural factors, such as the availability of food, competition with other zooplankton species, the presence of parasites, and the presence of both vertebrate and invertebrate predators (Yan *et al.* 2008).

Future directions and conclusions

These results provide a summary of the aquatic macroinvertebrate and zooplankton assemblages in acid-sensitive lakes in Kejimkujik National Park and National Historic Site and surrounding area in southwestern Nova Scotia. Although some of the overall trends of macroinvertebrate species richness with respect to varying pH were similar to results reported in other regions of eastern Canada, several differences were noted.

Some of the lakes in the study area had physical characteristics that differed from acid-sensitive lakes in other regions of eastern Canada, and these physical characteristics influenced the type and abundance of benthic macroinvertebrates that were collected. pH can vary spatially within each lake as well as seasonally due to runoff, with pulses of acidity in the spring and fall (Clair *et al.* 2007). These pulses also coincide with lower temperatures, and at these times of the year organisms may be less active and therefore more tolerant of their acidic environment (Stephenson and Mackie 1994). Although benthic microhabitats near the lake bed can have lower acidity than the upper water column (Grapentine and Rosenberg 1992), lakes in the study area are shallow with a large surface area which often allows for mixing throughout the open-water period. Therefore, benthic organisms would likely be exposed to high acidity throughout the active growth period in the summer.

All aquatic sampling methods have inherent biases in their sampling efficiencies for different invertebrate taxa. We employed multiple sampling methods in order to collect a wide range of taxa, but there was likely to have been variation in efficiency among the sampling methods with respect to particular taxa. Because the same suite of methods was used in all lakes, we assume the effects of this variation were consistent across the 20 study lakes, and we emphasize comparisons of invertebrate taxa patterns between lakes, rather than within lakes.

Our sampling methods, which were initially developed to collect benthic invertebrates from thick organic sediments in small Boreal Shield lakes in Ontario (McNicol *et al.* 1995b), may not be have been as suitable for lakes with rocky substrates. Although regional variation in species' habitat affinities may have contributed to particular differences between the findings from this study and reports from other regions (e.g., isopods, *H. azteca* distributions), substrate or other differences in the habitat also may have been a factor. Hoop sampling (visual searches in a confined area along the shoreline) worked particularly well in our lakes for sampling species of Trichoptera. Future studies should incorporate traditional benthic drag sampling with other methods such as kick and sweep, rock picking, or artificial substrates.

Carbone *et al.* (1998) successfully sampled macroinvertebrates in shallow, rocky littoral habitats using substrate cages filled with native rocks to match the rocky littoral substrate of sample lakes. This method might work well in Kejimkujik National Park and National Historic Site, where the littoral zone of many lakes is extremely shallow and consists of cobble and boulders. Many species collected in the study were rare (occurring in only one or two of the lakes) and had low counts. Increasing sampling effort, especially in the large lakes with varying substrate types, would reduce the likelihood of missed taxa.

Another interesting difference between the lakes in Kejimkujik National Park and National Historic Site and the lakes in the Boreal Shield in Ontario is the high concentration of dissolved organic carbon due to naturally occurring bogs and wetlands in the watersheds. The extremely dark waters of some lakes in the study area may benefit particular invertebrate species through physiology, protection from visual predators, or other reasons.

The data presented here establish a baseline for future monitoring in Kejimkujik National Park and National Historic Site as acid deposition continues to affect this region. Because the lakes are naturally acidic and are extremely vulnerable to additional acid inputs, recovery is slower than in other regions in eastern Canada affected by acid deposition (Clair *et al.* 2011). Additional effort may be required to reduce the impacts of acidification on the aquatic organisms that live in these ecosystems.

Acknowledgements

This study was funded by the Clean Air Regulatory Agenda (CARA) program of Environment Canada. Collections were made under scientific permits from Parks Canada and Fisheries and Oceans Canada. All animal handling followed procedures approved by the Environment Canada Animal Care Committee. We would like to thank Bohdan Bilyj (BIOTAX), who completed taxonomic identifications of macroinvertebrates, and the Sudbury Freshwater Co-op Unit at Laurentian University, where zooplankton identifications were completed. In addition, we thank Tom Clair and colleagues in the Water Science and Technology

Directorate, Environment Canada for providing water chemistry data. We thank Adam Martens and Miriam Morgan for field and lab assistance. Logistical support was provided by staff at Kejimkujik National Park and National Historic Site, Parks Canada.

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Received 30 August 2012
Accepted 20 February 2013

SUPPLEMENTARY TABLE 1. Abundance of zooplankton species observed in 15 lakes sampled in June 2009 and 2010 in Kejimkujik National Park and National Historic Site of Canada and vicinity in Nova Scotia. Abundance is presented as density (number of individuals/m^3). Lakes are arranged by pH from the lowest (Peskawa Lake) (pH = 4.8) to the highest (McGinty Lake) (pH = 6.6).

Classification and Family	Taxa Name	LAKE NAME															Number of lakes present	% of lakes present	mean density	min density	max density
		Peskawa	Frozen Ocean	Peskowesk	Big Dam West	George	North Cranberry	Back	Beaverskin	Grafton	Big Dam East	Upper Silver	Donnellan	Menchan	Turtle	McGinty					
	pH	4.8	4.9	5.0	5.1	5.1	5.5	5.7	5.8	6.2	6.2	6.3	6.5	6.5	6.6	6.6					
C. Branchiopoda, O. Diplostraca																					
Bosminidae	*Eubosmina tubicen*	4198	12055	10157	3128	1973	5206	1378	155	3622	8873	2755	66	45	2678	7232	15	100	4235	45	12055
	Bosmina freyi		4956		741	78		103			724		19			6830	7	47	1922	19	6830
	Bosmina liederi					129				132							2	13	131	129	132
Chydoridae	*Alona affinis*					26											1	7	26	26	26
	Chydorus sphaericus							35									1	7	35	35	35
Daphniidae	*Daphnia catawba*						905		595	1120	2897	6062		2188	3348	1205	8	53	2290	595	6062
	Daphnia longiremis									1185							1	7	1185	1185	1185
	Daphnia retrocurva							310				827			402		3	20	513	310	827
	Daphnia sp.													402			1	7	402	402	402
Holopediidae	*Holopedium gibberum*	1317	2947	4563	14480	931	2113	21705	492	66	2535	11848	1130	506	2277	24909	15	100	6121	66	24909
Leptodoridae	*Leptodora kindtii*					26							5				2	13	15	5	26
Ployphemidae	*Polyphemus pediculus*														134		1	7	134	134	134
Sididae	*Latona setifera*		134	86		26									268		4	27	128	26	268
	Diaphanosoma birgei	412	1205	2153	659	362	755	310	4742	1712	3803	5511	38	194	9242	14865	15	100	3064	38	14865
C. Maxillopoda, O. Calanoida																					
	Calanoid copepodid	23744	30144	12387	3949	5172	119708	7230	31093	27701	21710	6197	1507	2411	61173	60212	15	100	27622	1507	119708
	Calanoid nauplius	7904	36127	14451	25063	4138	17209	15415	49748	26382	40525	66231	4820	38635	938	22910	15	100	24700	938	66231
Diaptomidae	*Leptodiaptomus minutus*	4116	13019	4736	247	621	13808	10607	13965	9051	8330	58685	603	5089	8519	1205	15	100	10173	247	58685
	Skistodiaptomus oregonensis				3539					329	1087	1378				8035	5	33	2874	329	8035
	Aglaodiaptomus spatulocrenatus								466								1	7	466	466	466
Temoridae	*Epischura lacustris*															1205	1	7	1205	1205	1205
	Epischura lacustris copepodid			86							1268						2	13	677	86	1268
	Epischura nordenskioldi	905		258	165	26		35		66		827		74			8	53	294	26	905
	Epischura sp.	1152	268	344	1235	181		35	78	198		3582	9	45	670		12	80	650	9	3582
C. Maxillopoda, O. Cyclopoida																					
Cyclopidae	*Cyclopoid copepodid*	27	1741		1646	1940	1811	620	414	527	3079	4133	61	15	6829	9038	14	93	2277	15	9038
	Mesocyclops edax	82	670		412	52	453	138	26	395	362	551		74	134	1607	13	87	381	26	1607
	Cyclopoid nauplius	55	1473	258	1646	2199	2603	138	517	2633	3863	3031	1130	2545	10845	57803	15	100	6049	55	57803
	Tropocyclops extensus							69				551			268	804	4	27	423	69	804
	Tropocyclops prasinus			86		52											2	13	69	52	86

SUPPLEMENTARY TABLE 2. List of aquatic macroinvertebrate taxa observed in 20 lakes sampled in June 2009 and 2010 in Kejimkujik National Park and National Historic Site of Canada and vicinity in Nova Scotia. Lakes are arranged by pH from the most acidic (Big Red Lake) (pH 4.3) to the least acidic (McGinty Lake) (pH 6.6). Invertebrate taxa are organized by order, family, genus, and species (where possible) and include the total number of individuals captured in each lake as well as mean, minimum, and maximum counts and the percentage of lakes in which each taxon was observed.

Classification and Family	Taxa Name	LAKE NAME																				Number of lakes present	% of lakes present	mean count	min count	max count
		Big Red	Pebbleloggitch	Ben	Peskawa	Snake	Frozen Ocean	Peskowesk	Big Dam West	George	North Cranberry	Puzzle	Back	Beaverskin	Grafton	Big Dam East	Upper Silver	Donnellan	Menchan	Turtle	McGinty					
	pH	4.3	4.6	4.8	4.8	4.9	4.9	5.0	5.1	5.1	5.5	5.7	5.7	5.8	6.2	6.2	6.3	6.5	6.5	6.6	6.6					
O. Haplosclerida, Family Spongillidae														2								1	5	2.0	2	2
O. Arcellinida																										
Pseudodifflugiidae	*Pseudodifflugia*		1																			1	5	1.0	1	1
O. Nematoda		3	14		67	1	5	1	3	3	3	4	7	4	12	26	4	3		2	3	18	90	9.2	1	67
Subclass Oligochaeta, O. Haplotaxida																										
Enchytraeidae	*Enchytraeidae*		7		18		6	8	9	1	6	9	16	5	6	48				4		13	65	11.0	1	48
Lumbriculidae	*Stylodrilus heringianus*	3	11	24	11	4	17	33	56	7	24	26	31	50	15	5	38	98	93	53	31	20	100	31.5	3	98
Naididae	*Arcteonais lomondi*												1			1						2	10	1.0	1	1
	Chaetogaster diaphanus													2								1	5	2.0	2	2
	Dero digitata									1	5	1	4	1		1	4		1	3	4	10	50	2.5	1	5
	Haemonais waldvogeli																				2	1	5	2.0	2	2
	Nais simplex	2	24	5	2	2	7	3	2	1	4	11	18	4	53	1	8	1	5	2	18	20	100	8.7	1	53
	Naididae indet.											2				1						2	10	1.5	1	2
	Pristina leidyi		1									1	1				3		1	2		6	30	1.5	1	3
	Slavina appendiculata					2	1		1		10	6	8	4	40	13	2	3	1	2	6	14	70	7.1	1	40
	Specaria josinae														1							1	5	1.0	1	1
	Stylaria lacustris	76	176		1	4	56	5	39	5	22	66	38	19	70	21	19	9	7	8	20	19	95	34.8	1	176
	Vejdovskyella comata		1				6		1		1	2	2	1	14						3	9	45	3.4	1	14
Tubificidae	*Aulodrilus pigueti*										1											1	5	1.0	1	1
	Tubificinae			2			1		5	1	6	2	6	10			21	3	5	9		12	60	5.6	1	19
O. Tricladida																										
Dendrocoelidae	*Procotyla fluviatilis*				3					1												2	10	2.0	1	3
Dugesiidae	*Cura foremanii*										1		3				2	1	1	2		6	30	1.7	1	3
	Dugesia tigrina								1	1		3	3	1	2	3	1	1	23	1		11	55	3.6	1	23
Planariidae	*Phagocata woodworthi*		10		3		2			1		2							1			6	30	3.2	1	10
Subc. Hirudinea, O. Arhynchobdellida																										
Erpobdellidae	*Erpobdella punctata*							1					2	2				12	12	3		6	30	5.3	1	12

SUPPLEMENTARY TABLE 2. *(continued)*

Classification and Family	Taxa Name	LAKE NAME: Big Red	Pebbleloggitch	Ben	Peskawa	Snake	Frozen Ocean	Peskowesk	Big Dam West	George	North Cranberry	Puzzle	Back	Beaverskin	Grafton	Big Dam East	Upper Silver	Donnellan	Menchan	Turtle	McGinty	number of lakes present	% of lakes present	mean count	min count	max count
	pH	4.3	4.6	4.8	4.8	4.9	4.9	5.0	5.1	5.1	5.5	5.7	5.7	5.8	6.2	6.2	6.3	6.5	6.5	6.6	6.6					
	Mooreobdella fervida				2									8	1							3	15	3.7	1	8
	Mooreobdella melanostoma															2						1	5	2.0	2	2
	Erpobdellidae										1			1								2	10	1.0	1	1
Glossiphoniidae	*Glossiphonia complanata*																	1				1	5	1.0	1	1
	Helobdella elongata																	6	3			2	10	4.5	3	6
	Helobdella stagnalis												1		4			19	4	18	3	6	30	8.2	1	19
	Placobdella fusca																		1			1	5	1.0	1	1
	Placobdella hollensis																1					1	5	1.0	1	1
	Placobdella ornata												1								5	2	10	3.0	1	5
	Placobdella phalera														1				1			2	10	1.0	1	1
	Placobdella picta																			1		1	5	1.0	1	1
Hirudinidae	*Macrobdella decora*												2		2	2			1	1	1	6	30	1.5	1	2
O. Diplostraca, Subo. Cladocera																										
Chydoridae	*Alona*														1							1	5	1.0	1	1
	Eurycercus lamellatus		1		2	1					2				1						1	6	30	1.3	1	2
Daphniidae	*Daphnia*		1																			1	5	1.0	1	1
	Simocephalus serrulatus												1								1	2	10	1.0	1	1
	Ilyocryptus sordidus					1																1	5	1.0	1	1
	Latona parviremus									3				8	11							3	15	7.3	3	11
	Latona setifera									2		2		30		15						4	20	12.3	2	30
	Latonopsis				3																	1	5	3.0	3	3
	Leptadora kindtii																3					1	5	3.0	3	3
Macrothricidae	*Acantholeberis curvirostris*	27	13		7	13	4	30		3	3	2		2	20	12				28	7	14	70	12.2	2	30
	Ophryoxus gracilis	13	20		1		2	1		3	4	2		26	14	2		1		4	3	14	70	6.9	1	26
	Parophryoxus tubulatus														8							1	5	8.0	8	8
Sididae	*Sida crystallina*											1			3							2	10	2.0	1	3
Subcl. Copepoda																										
O. Cyclopoida	*Cyclopoida*									1		1	1	9		1						5	25	2.6	1	9

SUPPLEMENTARY TABLE 2. *(continued)*

Classification and Family	Taxa Name	LAKE NAME: Big Red	Pebbleloggitch	Ben	Peskawa	Snake	Frozen Ocean	Peskowesk	Big Dam West	George	North Cranberry	Puzzle	Back	Beaverskin	Grafton	Big Dam East	Upper Silver	Donnellan	Menchan	Turtle	McGinty	Number of lakes present	% of lakes present	mean count	min count	max count
	pH	4.3	4.6	4.8	4.8	4.9	4.9	5.0	5.1	5.1	5.5	5.7	5.7	5.8	6.2	6.2	6.3	6.5	6.5	6.6	6.6					
O. Amphipoda																										
Crangonyctidae	*Crangonyx richmondensis*	11	9	99			1					5	1	15			29	1		4	1	11	55	16.0	1	99
Hyalellidae	*Hyalella azteca*	39	31		18	54	46	20	224	62	61	59	87	77	249	107	33	340	239	89	358	19	95	115.4	18	358
O. Isopoda																										
Asellidae	*Caecidotea communis*	259	443	332	319	163	140	373	77	102	217	139	529	299	2	37	183	23	121	336	78	20	100	208.6	2	529
C. Ostracoda O. Podocopida																										
Candonidae	*Candona*														1							1	5	1.0	1	1
C. Arachnida, O. Trombidiformes																										
	Porolohmanella violacea		1																			1	5	1.0	1	1
Arrenuridae	*Arrenurus pseudocylindratus*		5		1						1	1			2							5	25	2.0	1	5
	Arrenurus superior													1								1	5	1.0	1	1
	Arrenurus sp. indet.	4	3		3	5			2	3			2	4	1	2		1	2			12	60	2.7	1	5
Axonopsidae	*Albia*						1		1		1											3	15	1.0	1	1
Hydrachnidae	*Hydrachna*					1																1	5	1.0	1	1
Hydrodromidae	*Hydrodroma despiciens*			1		1			1		3	1	2	1	1						2	9	45	1.4	1	3
Hygrobatidae	*Hygrobates*								1													1	5	1.0	1	1
Lebertiidae	*Lebertia*											1										1	5	1.0	1	1
Limnesiidae	*Limnesia maculata*		3					1			1	2	2	2							1	7	35	1.7	1	3
	Limnesia undulata		3						1							1	1					4	20	1.5	1	3
	Limnesia species indet.		1								1											2	10	1.0	1	1
Limnocharidae	*Limnochares americana*	19	1	1		14		6	3		2	3		3	1			1		1	1	13	65	4.3	1	19
	Limnochares aquatica		1	1	1	2					1	2				5		1		1	3	10	50	1.8	1	5
Oxidae	*Frontipoda americana*								1													1	5	1.0	1	1
Pionidae	*Piona*		1			1	1		1			1			1							6	30	1.0	1	1
Pseudohydryphantidae	*Pseudohydryphantes*																				1	1	5	1.0	1	1
Unionicolidae	*Neumania*																				2	1	5	2.0	2	2
	Unionicola crassipes		3				1			1	3				5					1	1	7	35	2.1	1	5

SUPPLEMENTARY TABLE 2. *(continued)*

Classification and Family	Taxa Name	LAKE NAME																				Number of lakes present	% of lakes present	mean count	min count	max count
		Big Red	Pebbleloggitch	Ben	Peskawa	Snake	Frozen Ocean	Peskowesk	Big Dam West	George	North Cranberry	Puzzle	Back	Beaverskin	Grafton	Big Dam East	Upper Silver	Donnellan	Menchan	Turtle	McGinty					
	pH	4.3	4.6	4.8	4.8	4.9	4.9	5.0	5.1	5.1	5.5	5.7	5.7	5.8	6.2	6.2	6.3	6.5	6.5	6.6	6.6					
O. Collembola																										
Bourletiellidae	*Bourletiella spinata*				1				1	1												3	15	1.0	1	1
Isotomidae	*Isotomurus*														1							1	5	1.0	1	1
O. Odonata, Subo. Anisoptera																										
Aeshna clepsydra					1																	1	5	1.0	1	1
Aeshnidae																										
	Aeshna eremita		1	2							2			1			1					5	25	1.4	1	2
	Aeshnidae										1			1								2	10	1.0	1	1
	Basiaeschna janata										1	1			1			1			1	5	25	1.0	1	1
	Boyeria grafiana	1		1	1		2					1							1		1	7	35	1.1	1	2
Corduliidae	*Cordulia shurleffi*	7	3	24		2		2		1		4	5	6	2	1				3	15	13	65	5.8	1	24
	Cordulidae	4						1														2	10	2.5	1	4
	Didymops transversa						1		2	1	1								1		1	6	30	1.2	1	2
	Dorocordulia lepida	9			1		5	4				5						1		4	4	8	40	4.1	1	9
	Epitheca cynosura		3		2	1			2	2	11	2	2	1	2	1		2	3		9	14	70	3.1	1	11
	Macromia illinoiensis																			2		1	5	2.0	2	2
	Somatochlora incurvata								1													1	5	1.0	1	1
	Somatochlora williamsoni										2	2	2									3	15	2.0	2	2
Gomphidae	*Gomphus exilis*				2	2	16		9	5	13	1	1	3	1	7		5			2	13	65	5.2	1	16
	Gomphus spicatus		1				1			3								1	1			5	25	1.4	1	3
	Hagenius brevistylus						4															1	5	4.0	4	4
Libellulidae	*Celithemis eponina*										4	2		18		41	1	1	1	1		8	40	8.6	1	41
	Ladona julia	3	16		2	6		5		6	10	8	1	6	5	2				3	2	14	70	5.4	1	16
	Leucorrhinia frigida										1							1			6	3	15	2.7	1	6
	Leucorrhinia hudsonica			19										4			1		1			4	20	6.3	1	19
	Libellula incesta	3	1		2	1	2	1	1		7	10	1	5	2	1		5		1	1	16	80	2.8	1	10
	Libellulidae		1			1												4			2	4	20	2.0	1	4
	Sympetrum obtrusum		2							5					3							3	15	3.3	2	5
	Sympetrum vicinum		1								2			3	3							4	20	2.3	1	3

SUPPLEMENTARY TABLE 2. *(continued)*

Classification and Family	Taxa Name	LAKE NAME																				Number of lakes present	% of lakes present	mean count	min count	max count
		Big Red	Pebbleloggitch	Ben	Peskawa	Snake	Frozen Ocean	Peskowesk	Big Dam West	George	North Cranberry	Puzzle	Back	Beaverskin	Grafton	Big Dam East	Upper Silver	Donnellan	Menchan	Turtle	McGinty					
	pH	4.3	4.6	4.8	4.8	4.9	4.9	5.0	5.1	5.1	5.5	5.7	5.7	5.8	6.2	6.2	6.3	6.5	6.5	6.6	6.6					
O. Odonata, Subo. Zygoptera																										
Coenagrionidae	*Argia moesta*						2															1	5	2.0	2	2
	Argia violacea	1															1					2	10	1.0	1	1
	Chromagrion conditum				1						2											2	10	1.5	1	2
	Coenagrionidae																	1				1	5	1.0	1	1
	Enallagma aspersum	3		2							2	1		15			13	1				7	35	5.3	1	15
	Enallagma geminatum	4	13		3				2		2	8	1	5		6			3	1		11	55	4.4	1	13
	Enallagma hageni	1	5	6	1	1			1							2			1	2	1	10	50	2.1	1	6
	Enallagma vesperum	2	3			1			1		1			1		3	1	3	4	1	2	12	60	1.9	1	4
	Ischnura verticalis	3	3		2	1	4	3	1	1					1		3	5	1			12	60	2.3	1	5
Lestidae	*Lestes vigilax*																	1				1	5	1.0	1	1
O. Ephemeroptera																										
Baetidae	*Procloeon*														1							1	5	1.0	1	1
Caenidae	*Caenis diminuta*	3	50		1	24	63		13	4	2	11		10	39	16				2	26	14	70	18.9	1	63
Ephemerellidae	*Eurylophella bicolor*	7			46		5	6	27	7			7	2			1	29	62	4		12	60	16.9	1	62
	Eurylophella minimella				3																	1	5	3.0	3	3
	Eurylophella prundentalis				6			4	2				2	2		1	1	1	2	1		10	50	2.2	1	6
	Eurylophella temporalis		1												2		2	5	21	3		6	30	5.7	1	21
Ephemeridae	*Eurylophella*																1					1	5	1.0	1	1
	Hexagenia limbata		5		1			3	2	3	5	1				11		6				9	45	4.1	1	11
Heptageniidae	*Stenacron interpunctatum*	1	1		1		2		1	1					1		1	4	2	3	2	12	60	1.7	1	4
Leptophlebiidae	*Paraleptophlebia*															1			1			2	10	1.0	1	1
Siphlonuridae	*Siphlonurus*				3				3	1				2	3	18		1				7	35	4.4	1	18
O. Plecoptera																										
Perlidae	*Acroneuria lycorias*												1					2	1			3	15	1.3	1	2
Leuctridae	*Leuctra tenuis*				11			2	7	20	1		2	1			9	40	7	5		11	55	9.5	1	40
O. Lepidoptera																										
Crambidae	*Eoparargyractis*								1							1						2	10	1.0	1	1
	Paraponyx															1						1	5	1.0	1	1

SUPPLEMENTARY TABLE 2. *(continued)*

Classification and Family	Taxa Name	LAKE NAME																				Number of lakes present	% of lakes present	mean count	min count	max count
		Big Red	Pebbleloggitch	Ben	Peskawa	Snake	Frozen Ocean	Peskowesk	Big Dam West	George	North Cranberry	Puzzle	Back	Beaverskin	Grafton	Big Dam East	Upper Silver	Donnellan	Menchan	Turtle	McGinty					
	pH	4.3	4.6	4.8	4.8	4.9	4.9	5.0	5.1	5.1	5.5	5.7	5.7	5.8	6.2	6.2	6.3	6.5	6.5	6.6	6.6					
O. Neuroptera																										
Sisyridae	*Climacia areolaris*		1	1									3							1	1	5	25	1.4	1	3
O. Megaloptera																										
Corydalidae	*Nigronia serricornis*			1									1			1		3		3		5	25	1.8	1	3
Sialidae	*Sialis*			2						1												2	10	1.5	1	2
O. Hemiptera																										
Corixidae	*Corixidae*			1					3													2	10	2.0	1	3
Veliidae	*Rhagovelia obesa*													1								1	5	1.0	1	1
Gerridae	*Rheumatobates rileyi*												22	4			187					3	15	71.0	4	187
	Trepobates								1													1	5	1.0	1	1
O. Trichoptera																										
Dipseudopsidae	*Phylocentropus*		10		2	1					2		1	1				1	1			8	40	2.4	1	10
Helicopsychidae	*Helicopsyche borealis*		1										3						1			3	15	1.7	1	3
Hydroptilidae	*Hydroptila*		5						10	2	2				10	10		1				7	35	5.7	1	10
	Orthotrichia													1								1	5	1.0	1	1
	Oxyethira	20	17	5	8	3	42	3	20		10	10	23		13	22	1	3		11	5	17	85	12.7	1	42
Lepidostomatidae	*Lepidostoma*	17		1	7		7		6	2	14		44	8		3	7		241	10		13	65	28.2	1	241
Leptoceridae	*Ceraclea maculata*				2																	1	5	2.0	2	2
	Ceraclea spongillovorax			1																		1	5	1.0	1	1
	Ceraclea transversa							1		1						4						3	15	2.0	1	4
	Mystacides interjecta	2	6		5	3	3		1	9	5	1			5				41			11	55	7.4	1	41
	Mystacides sepulchralis													1								1	5	1.0	1	1
	Nectopsyche pavida	3	11		5	16	54	4	4	8	22	7	71		12	7	11	2	87	62	3	18	90	21.6	2	87
	Oecetis cinerascens						1		3		1		1		1			2	1	2	1	9	45	1.4	1	3
	Oecetis osteni		35	1	3	3	13	1	16	10	1		12			1	1		8			13	65	8.1	1	35
	Oecetis porteri				1		25		10	10	12	1	7			5		3	1	1		11	55	6.9	1	25
	Oecetis sp.1 inconspicua cmplx					2									1				2			3	15	1.7	1	2
	Oecetis sp.2 inconspicua cmplx		36		5	1	11	3		1	21	8	18	24	10	6	2	10	10	2		16	80	10.5	1	36
	Oecetis sp.3 inconspicua cmplx						3						1				6					3	15	3.3	1	6
	Triaenodes injustus			1					1		1		2				1		3	1		7	35	1.4	1	3

SUPPLEMENTARY TABLE 2. *(continued)*

Classification and Family	Taxa Name	LAKE NAME																				Number of lakes present	% of lakes present	mean count	min count	max count
		Big Red	Pebbleloggitch	Ben	Peskawa	Snake	Frozen Ocean	Peskowesk	Big Dam West	George	North Cranberry	Puzzle	Back	Beaverskin	Grafton	Big Dam East	Upper Silver	Donnellan	Menchan	Turtle	McGinty					
	pH	4.3	4.6	4.8	4.8	4.9	4.9	5.0	5.1	5.1	5.5	5.7	5.7	5.8	6.2	6.2	6.3	6.5	6.5	6.6	6.6					
	Triaenodes nox		1							1		1										3	15	1.0	1	1
	Triaenodes species indet.		1																			1	5	1.0	1	1
Limnephilidae	*Leptoceridae*																		1			1	5	1.0	1	1
	Glyphopsyche irrorata	21	2	3			6		4		11	10	72	3			8		30	3	10	13	65	14.1	2	72
	Grammotaulius																		1			1	5	1.0	1	1
	Hydatophylax			5												4			2			3	15	3.7	2	5
	Limnephilus	22	44	5	7	18	7	2	47		10	14	5	2				5	11	1	1	16	80	12.5	1	47
	Phanocelia canadensis	1					3															2	10	2.0	1	3
	Platycentropus amicus	2	6	3	1	8	3	6	2	2	4	9	3		1			1	5		6	16	80	3.9	1	9
Molannidae	*Molanna ulmerina-uniophila*	1	16	4		2			4	2				1		1			1			9	45	3.6	1	16
Phryganeidae	*Agrypnia straminea*	6	5							1	6	3	1	2		1					1	9	45	2.9	1	6
	Banksiola crotchi				1			1								3	2	1		1		6	30	1.5	1	3
	Banksiola smithi	2	3	1		1		2				1	4	1								8	40	1.9	1	4
Polycentropodidae	*Nyctiophylax*															3				1		2	10	2.0	1	3
	Polycentropus	7	8	1	6	3	1		3	4	1	2			3		1	6		2	1	15	75	3.3	1	8
Sericostomatidae	*Agarodes distinctus*	10	3			1		2	3		12		15		1	1	1	5	4	2		13	65	4.6	1	15
O. Coleoptera																										
Chrysomelidae	*Donacia*		1															4	1			3	15	2.0	1	4
	Pyrrhalta												1									1	5	1.0	1	1
Curculionidae	*Phyllobius oblongus*																		19			1	5	19.0	19	19
Dytiscidae	*Coptotomus*				1																	1	5	1.0	1	1
	Matus ovatus		1																			1	5	1.0	1	1
	Neoporus undulatus	3	11		9		2	4	2				1				1	3				9	45	4.0	1	11
Elmidae	*Ancyronyx variegata*				1			2				6	4								4	5	25	3.4	1	6
	Dubiraphia vittata		50			182	51		4	45	1		19		39			14		121	111	11	55	57.9	1	182
	Macronychus glabratus																1		6	2		3	15	3.0	1	6
	Stenelmis – larvae	162		1		11	2	10	29				1				2	5	7	2		11	55	21.1	1	162
	Stenelmis crenata adult	27	53		48			1		2	8	4	2	1		1						10	50	14.7	1	53
	Stenelmis musgravei - adult														1							1	5	1.0	1	1
Gyrinidae	*Gyrinus*																		1			1	5	1.0	1	1

SUPPLEMENTARY TABLE 2. *(continued)*

Classification and Family	Taxa Name	LAKE NAME																				Number of lakes present	% of lakes present	mean count	min count	max count
		Big Red	Pebbleloggitch	Ben	Peskawa	Snake	Frozen Ocean	Peskowesk	Big Dam West	George	North Cranberry	Puzzle	Back	Beaverskin	Grafton	Big Dam East	Upper Silver	Donnellan	Menchan	Turtle	McGinty					
	pH	4.3	4.6	4.8	4.8	4.9	4.9	5.0	5.1	5.1	5.5	5.7	5.7	5.8	6.2	6.2	6.3	6.5	6.5	6.6	6.6					
Hydrophilidae	*Berosus*	11	30		5	13	6	9	4	7	3				7							10	50	9.5	3	30
Psephenidae	*Ectopria nervosa*										1			2				5	7	2		5	25	3.4	1	7
O. Diptera																										
Ceratopogonidae	*Bezzia*	1	20	5	3	3	4	7	4	1	2	7	2	5	11	10	2	3	1	9	5	20	100	5.3	1	20
	Dasyhelea														1			1	2		1	4	20	1.3	1	2
	Monohelea		2																1			2	10	1.5	1	2
	Palpomyia	1							5							2						3	15	2.7	1	5
	Probezzia	5	5		2	3	1		3	1					3				2			9	45	2.8	1	5
	Sphaeromias												4									1	5	4.0	4	4
Chaoboridae	*Chaoborus punctipennis*					2																1	5	2.0	2	2
Chironomidae	*Chironomidae*	16	26	13	10	11	5	5	19	2	12	6	19	9	8	15	14	13	7	13	33	20	100	12.8	2	33
Dolichopodidae	*Rhaphium*														2							1	5	2.0	2	2
Emphididae	*Hemerodromia*										3	1				1			4			4	20	2.3	1	4
Tabanidae	*Chrysops excitans*		3	1	2						6	1	1		1			1	1			9	45	1.9	1	6
C. Gastropoda																										
Ancylidae	*Ferrissia fragilis*		22	26	37	4	22	10	9	31	25	15	78	16	1	9	7			7	1	17	85	18.8	1	78
	Gyraulus deflectus																	8	7	1		3	15	5.3	1	8
Hydrobiidae	*Amnicola limosa*														66	3		105	21	17	286	6	30	83.0	3	286
	Cincinnatia integra								2													1	5	2.0	2	2
Planorbidae	*Helisoma anceps*															1		1				2	10	1.0	1	1
	Menetus dilatatus																1	22	1	6	22	5	25	10.4	1	22
	Physa																1	11				2	10	6.0	1	11
	Planorbella trivolvis															11						1	5	11.0	11	11
	Planorbella campanulata																	2				1	5	2.0	2	2
	Probythinella emarginata														6							1	5	6.0	6	6
Valvatidae	*Valvata perdepressa*														1							1	5	1.0	1	1
	Valvata sincera																		1			1	5	1.0	1	1
Viviparidae	*Campeloma decisum*														4	2	2	6	2	1	16	7	35	4.7	1	16

SUPPLEMENTARY TABLE 2. *(continued)*

Classification and Family	Taxa Name	LAKE NAME																				Number of lakes present	% of lakes present	mean count	min count	max count
		Big Red	Pebbleloggitch	Ben	Peskawa	Snake	Frozen Ocean	Peskowesk	Big Dam West	George	North Cranberry	Puzzle	Back	Beaverskin	Grafton	Big Dam East	Upper Silver	Donnellan	Menchan	Turtle	McGinty					
	pH	4.3	4.6	4.8	4.8	4.9	4.9	5.0	5.1	5.1	5.5	5.7	5.7	5.8	6.2	6.2	6.3	6.5	6.5	6.6	6.6					
C. Bivalvia, O. Veneroida																										
Pisidiidae	*Musculium lacustre*							1														1	5	1.0	1	1
	Musculium partumeium														3		1	3	4		67	5	25	15.6	1	67
	Musculium securis																		1			1	5	1.0	1	1
	Pisidium adamsi																				1	1	5	1.0	1	1
	Pisidium casertanum					5		5	12	4	14	5	3	1	20	4	1	23	25	5	35	15	75	10.8	1	35
	Pisidium ferrugineum										4	1			16	5		42	27	7	48	8	40	18.8	1	48
	Pisidium nitidum										4	24			4			1				4	20	8.3	1	24
	Pisidium rotundatum														9			1				2	10	5.0	1	9
	Pisidium variabile														7		3	84	4	10	14	6	30	20.3	3	84
	Pisidium ventricosum														1			47	1	2		4	20	12.8	1	47
	Pisidium species indet.						4				11		22		50			14			55	6	30	26.0	4	55

An Illustrated Key to the Mandibles of Small Mammals of Eastern Canada

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Fauteux, Dominique, Gilles Lupien, François Fabianek, Jonathan Gagnon, Marion Séguy, and Louis Imbeau. 2014. An illustrated key to the mandibles of small mammals of eastern Canada. Canadian Field-Naturalist 128(1): 25–37.

Skulls are often used to identify small mammals, and most identification keys to small mammals have been developed on the assumption that whole skulls will be available. However, the skulls of small mammals are seldom found intact in predator pellets or nests, and the bones of several individuals are often scattered and mixed, making counting impossible without the use of a specific cranial part. In addition, only a few keys include all the species found in the eastern provinces of Canada.

Mandibles readily resist degradation by the gastric acids of both avian and mammalian predators and are often found intact in food caches of mustelids and in bat hibernacula. We therefore designed an illustrated dichotomous key to small mammals (mean mass <5 kg) of eastern Canada based on diagnostic mandible characters (including the teeth and one dentary bone). We identified and confirmed diagnostic characters to distinguish 55 species from the orders Lagomorpha, Rodentia, Soricomorpha, Carnivora, and Chiroptera. These diagnostic characters are based on a review of the literature and were confirmed by measurements performed on both museum and trapped specimens. In order to facilitate identification, photographic illustrations are provided for each couplet of the key.

The ability to identify small mammals using their mandibles will reduce the number of skull components needed and has proven to be a useful tool in the study of the diet of predators. This key may also be helpful in identifying bats in the genera *Myotis*, *Perimyotis*, and *Eptesicus*, which are presently affected by the spread of white-nose syndrome (caused by *Pseudogymnoascus destructans*) throughout the eastern part of Canada.

Key Words: Lagomorpha; Rodentia; Soricomorpha; Carnivora; Chiroptera; shrews; moles; voles; lemmings; mice; bats; hares; weasels; lower jaw; skull; dentary; eastern Canada

Introduction

Small mammals consumed by predators are particularly difficult to identify because their skulls are often physically damaged or they have been degraded by gastric acids (Mayhew 1977). Cranial bones that resist degradation often disassociate from the larger component they were affixed to and are often found scattered in predator scats, pellets, or nests (Buidin *et al.* 2007; Khalafalla and Iudica 2010). They may also be found as concentrations of loose bones near caves or other shelters used by predators (Buden 1974). Predators such as mustelids have "food caches" in which they store carcasses for later consumption (Oksanen *et al.* 1985). As a result, prey remains may be disassociated and may accumulate.

Several published keys to small mammal skulls are based on the assumption that the whole skull is available (van Zyll de Jong 1983; Glass and Thies 1997; Lupien 2001, 2002; Nagorsen 2002; Chapman *et al.* 2007), but this is rarely the case with prey remains (Mollhagen *et al.* 1972; Buden 1974; Balciauskiene *et al.* 2002). Furthermore, loose bones of different individual prey items are often mixed. The minimum number of individuals is a derived unit of abundance often used in paleozoology (Lyman 2008). By using a single skull component, this method avoids overestimating species abundance in bone aggregations. The mandible has been proposed as a useful cranial component for identifying groups of mammals (Roest 1991; Balciauskiene *et al.* 2002), but it has rarely been used to identify mammals to the species level, except for shrews (Repenning 1967; Carraway 1995).

The mandible, or lower jaw, is composed of teeth and a pair of dentary bones (Figure 1). The teeth of the mandible are often referred to as the lower dentition, and each tooth is identified with a lower case letter (i.e., p3 for the third premolar). For the present article, we focused on the mandible and thus omitted the term "lower". Because the left and right dentary often separate as a result of degradation, it is imperative that the same dentary bone (i.e., left or right, but not both) be used for counting purposes.

Several diagnostic characters make the mandible an ideal tool for identifying most mammalian species that have very few but sturdy bones. The size, the dental formulae, and the occlusal patterns of the molar enamel are key characteristics that are often used in keys to skulls (Repenning 1967; Glass and Thies 1997; Lupien 2002; Nagorsen 2002). Furthermore, diagnostic characters of the dentary bones are found on both the anterior and the posterior parts. The size and shape of the lower edge of the ramus and the position of the mental and dental foramina, as well as the size and shape of the condylar, coronoid, and angular processes, are useful characters requiring only a few metric measurements (Roest 1991; Carraway 1995).

We present an identification key to the mandibles of all established small mammals (mean mass of <5 kg) of eastern Canada to assist in the identification of prey remains and other types of loose bones when skulls are incomplete or damaged. Each criterion mentioned in the couplets of the key is illustrated by a picture as a visual support. A glossary and the general nomenclature are also provided.

Methods

According to Merritt (2010), mammals may be categorized as small when the average mass of the species is less than 5 kg. Based on this criterion, we selected all the small mammals established in the provinces of Ontario, Quebec, Newfoundland and Labrador, Prince Edward Island, New Brunswick, and Nova Scotia (Peterson 1966; Banfield 1974; Dobbyn 1994; Desrosiers *et al.* 2002; Naughton 2012). The general taxonomy used in the key is listed in Table 1.

This key summarizes all diagnostic mandible characters that we have found in the literature for the orders Lagomorpha (Roest 1991), Rodentia (Klingener 1963; Phillips and Oxberry 1972; Grayson *et al.* 1990; Roest 1991; Lupien 2002; Chapman *et al.* 2007), Soricomorpha (Hallet 1978; Yates and Schmidly 1978; van Zyll de Jong 1983; Carraway 1995; Glass and Thies 1997; Lupien 2001), Carnivora (Roest 1991; Glass and Thies 1997), and Chiroptera (Gaudin *et al.* 2011). Certain species were very difficult to distinguish using the morphologic features of the mandible alone. Therefore, we included morphometric measurements such as the length of the mandible, the length of the mandibular tooth row, and the height of the coronoid process when two species or groups of species could be distinguished only by size.

We validated the mandible characteristics presented in this key by studying specimens from Ontario, Quebec, Newfoundland and Labrador, Prince Edward Island, New Brunswick, and Nova Scotia preserved in the Canadian Museum of Nature and Université Laval. Morphometric measurements were validated on 10 specimens of each species when possible. Otherwise, all specimens available were used. We further extracted a sample of reference mandibles from complete frozen specimens, in collaboration with the Ministère du Développement durable, de l'Environnement, de la Faune et des Parcs du Québec and the Université du Québec à Rimouski, and from specimens trapped during a related study (Fauteux *et al.* 2012). The relevance of the diagnostic characters in identifying prey remains was validated by Séguy (2010) using nest remains to quantify the diet of Northern Saw-whet Owls (*Aegolius acadicus*).

Results and Discussion

We found that 55 of the 60 small mammal species of eastern Canada could be identified from their mandibles. The White-footed Mouse (*Peromyscus leucopus*) and the Deer Mouse (*P. maniculatus*) could not be identified to the species level, because their mandibles are identical. Although both *Peromyscus* species may be differentiated using several skull measurements, biochemical and genetic markers are probably the only reliable methods to date (Aquadro and Patton 1980; Rich *et al.* 1996). Similarly, three species of lagomorphs (i.e., *Lepus arcticus*, *L. europaeus*, and *L. townsendii*) could not be distinguished using the mandibles alone.

Consulting species' distribution may facilitate identification of small mammals (Banfield 1974; Desrosiers *et al.* 2002; Naughton 2012). For example, *Sciurus*

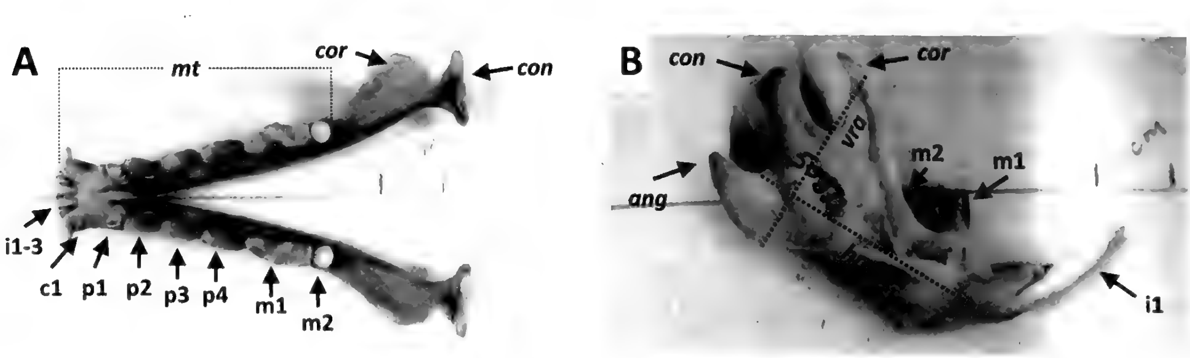

FIGURE 1. (*A. Labial view; B. Occlusal view*) The mandibles of carnivores (*Martes americana*) (A) and rodents (*Ondatra zibethicus*) (B). Labels refer to the incisor (i), canine (c), premolar (p), molar (m), mandibular tooth row (*mt*), coronoid process (*cor*), condyle (*con*), angular process (*ang*), vertical ramus (*vra*), and horizontal ramus (*hra*).

TABLE 1. Common and scientific names of the small mammals <5 kg in eastern Canada identified in the dichotomous key (Peterson 1966; Banfield 1974; Wilson and Reeder 2005; Hoofer *et al.* 2006; Naughton 2012; ITIS 2013).

Order	Family	Scientific name	Common name (English)	Nom commun (français)
Rodentia	Cricetidae	*Dicrostonyx hudsonius*	Ungava Collared Lemming	Lemming d'Ungava
		Microtus chrotorrhinus	Rock Vole	Campagnol des rochers
		Microtus pennsylvanicus	Meadow Vole	Campagnol des champs
		Microtus pinetorum	Woodland Vole	Campagnol sylvestre
		Myodes gapperi	Southern red-backed Vole	Campagnol à dos roux de Gapper
		Myodes glareolus	Bank Vole	Campagnol roussâtre
		Ondatra zibethicus	Common Muskrat	Rat-musqué commun
		Peromyscus leucopus	White-footed Mouse	Souris à pattes blanches
		Peromyscus maniculatus	Deer Mouse	Souris sylvestre
		Phenacomys ungava	Eastern Heather Vole	Phénacomys
		Synaptomys borealis	Northern Bog Lemming	Lemming des tourbières
		Synaptomys cooperi	Southern Bog Lemming	Lemming de Cooper
	Dipodidae	*Napaeozapus insignis*	Woodland Jumping Mouse	Zapode des bois
		Zapus hudsonius	Meadow Jumping Mouse	Zapode des champs
	Erethizontidae	*Erethizon dorsatum*	North American Porcupine	Porc-épic d'Amérique
	Muridae	*Mus musculus*	Common Mouse	Souris commune
		Rattus norvegicus	Norway Rat	Rat surmulot
	Sciuridae	*Glaucomys sabrinus*	Northern Flying Squirrel	Grand polatouche
		Glaucomys volans	Southern Flying Squirrel	Petit polatouche
		Marmota monax	Woodchuck	Marmotte commune
		Poliocitellus franklinii	Franklin's Ground Squirrel	Spermophile de Franklin
		Tamias minimus	Least Chipmunk	Tamia mineur
		Tamias striatus	Eastern Chipmunk	Tamia rayé
		Tamiasciurus hudsonicus	Red Squirrel	Écureuil roux
		Sciurus carolinensis	Eastern Gray Squirrel	Écureuil gris
		Sciurus niger	Eastern Fox Squirrel	Écureuil fauve
Lagomorpha	Leporidae	*Lepus americanus*	Snowshow Hare	Lièvre d'Amérique
		Lepus arcticus	Arctic Hare	Lièvre arctique
		Lepus europaeus	European Hare	Lièvre d'Europe
		Lepus townsendii	White-tailed Jackrabbit	Lièvre de Townsend
		Sylvilagus floridanus	Eastern Cottontail	Lapin à queue blanche
Carnivora	Canidae	*Urocyon cinereoargenteus*	Grey Fox	Renard gris
		Vulpes lagopus	Arctic Fox	Renard arctique
		Vulpes vulpes	Red Fox	Renard roux
	Mephitidae	*Mephitis mephitis*	Striped Skunk	Moufette rayée
	Mustelidae	*Martes americana*	American Marten	Martre d'Amérique
		Martes pennanti	Fisher	Pékan
		Mustela erminea	Ermine	Hermine
		Mustela frenata	Long-tailed Weasel	Belette à longue queue
		Mustela nivalis	Least Weasel	Belette pygmée

TABLE 1. (*continued*) Common and scientific names of the small mammals <5 kg in eastern Canada identified in the dichotomous key (Peterson 1966; Banfield 1974; Wilson and Reeder 2005; Hoofer *et al.* 2006; Naughton 2012; ITIS 2013).

Order	Family	Scientific name	Common name (English)	Nom commun (français)
		Neovison vison	American Mink	Vison d'Amérique
Soricomorpha	Soricidae	*Blarina brevicauda*	Northern Short-tailed Shrew	Grande musaraigne
		Sorex arcticus	Arctic Shrew	Musaraigne arctique
		Sorex cinereus	Cinereous Shrew	Musaraigne cendrée
		Sorex dispar	Long-tailed Shrew	Musaraigne longicaude
		Sorex fumeus	Smoky Shrew	Musaraigne fuligineuse
		Sorex hoyi	North American Pygmy Shrew	Musaraigne pygmée
		Sorex maritimensis	Maritime Shrew	Musaraigne des Maritimes
		Sorex palustris	North American Water Shrew	Musaraigne palustre
	Talpidae	*Condylura cristata*	Star-nosed Mole	Condylure à nez étoilé
		Parascalops breweri	Hairy-tailed Mole	Taupe à queue velue
		Scalopus aquaticus	Eastern Mole	Taupe à queue glabre
Chiroptera	Vespertilionidae	*Eptesicus fuscus*	Big Brown Bat	Grande chauve-souris brune
		Lasionycteris noctivagans	Silver-haired Bat	Chauve-souris argentée
		Lasiurus borealis	Eastern Red Bat	Chauve-souris rousse
		Lasiurus cinereus	Hoary Bat	Chauve-souris cendrée
		Myotis leibii	Eastern Small-footed Myotis	Chauve-souris pygmée
		Myotis lucifugus	Little Brown Myotis	Petite chauve-souris brune
		Myotis septentrionalis	Northern Myotis	Chauve-souris nordique
		Perimyotis subflavus	Tri-colored Bat	Pipistrelle de l'Est

niger are found only in extreme southern Ontario, and the distribution of *Sorex maritimensis* is restricted to New Brunswick and Nova Scotia.

The mandible is highly polymorphic between and within orders. The order Soricomorpha can be distinguished from other orders because the canine is similar in size to the premolars and the angular process is long and slender (Figure 2B) (key section D). In Lagomorpha, the large angular process and the very small coronoid process are probably the most distinctive characters (Figure 3A) (key section B). In contrast, species of the order Rodentia have a well-developed coronoid process, often with complex occlusal patterns on the molars (Figures 3B) (key section C). Carnivores have large canines and a coronoid process that is disproportionately larger than the condyle and the angular process (Figure 4B) (key section E). Species from the order Chiroptera are mainly characterized by the relatively small vertical ramus and the conspicuous bump on the lower edge of the horizontal ramus beneath the canine (Figure 5B) (key section F).

In some cases, mandibles may be broken and/or teeth may be missing. To address this problem, we provide two or more criteria. However, we struggled to find more than one mandibular characteristic in certain groups of species. In the orders Lagomorpha and Carnivora, only the length of the mandibular tooth row and the height of the coronoid process may be used effectively to distinguish the hares (*Lepus* spp.) and the weasels (*Mustela* spp.). Voles and lemmings may be more effectively differentiated with dental criteria, and identifications may become difficult when the teeth are missing (Banfield 1974; Lupien 2002). Although identifications using heavily degraded mandibles (e.g.,

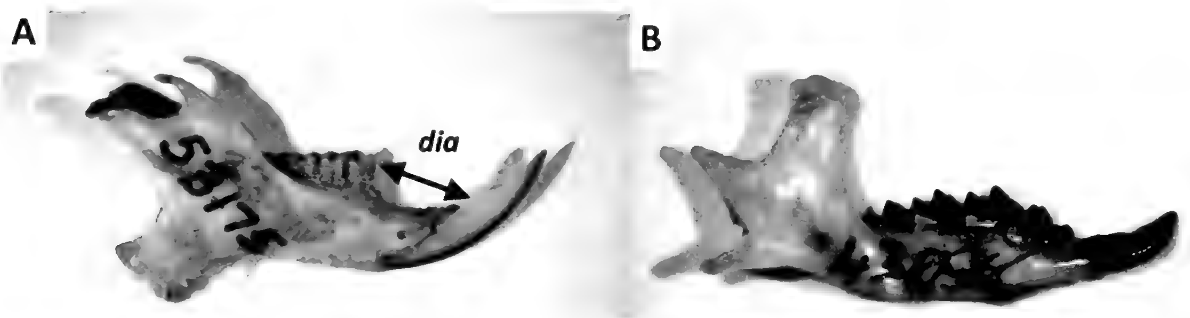

Figure 2. (*labial view*) Dentary bone of rodents with a large diastema (*dia*) (*Glaucomys volans*) (A), and soricomorphs (*Blarina brevicauda*) (B).

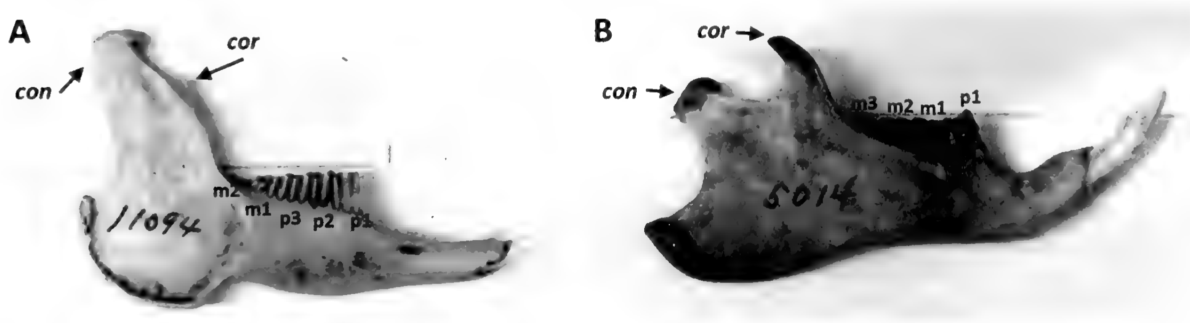

Figure 3. (*labial view*) Coronoid process (*cor*) and condyle (*con*) of lagomorphs (*Lepus arcticus*) (A) and rodents (*Marmota monax*) (B).

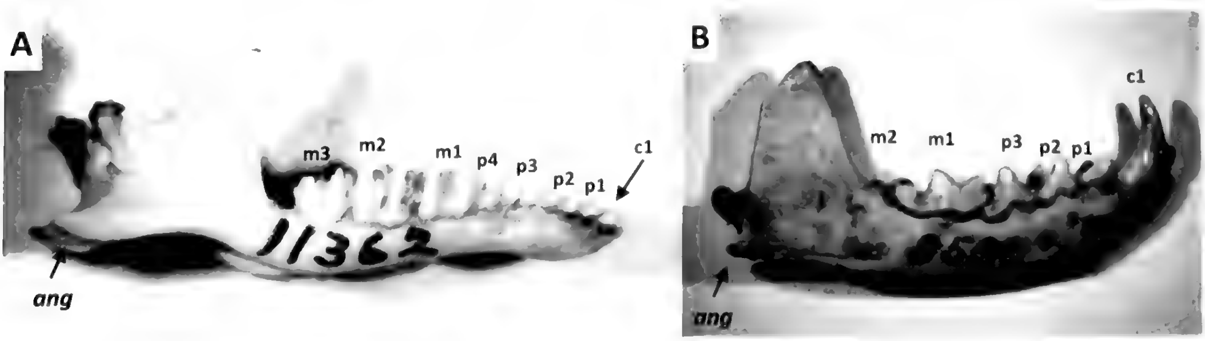

Figure 4. (*labial view*) Size of the angular process as well as the size of the canine compared to the adjacent premolar in soricomorphs (*Parascalops breweri*) (A) and carnivores (*Neovison vison*) (B).

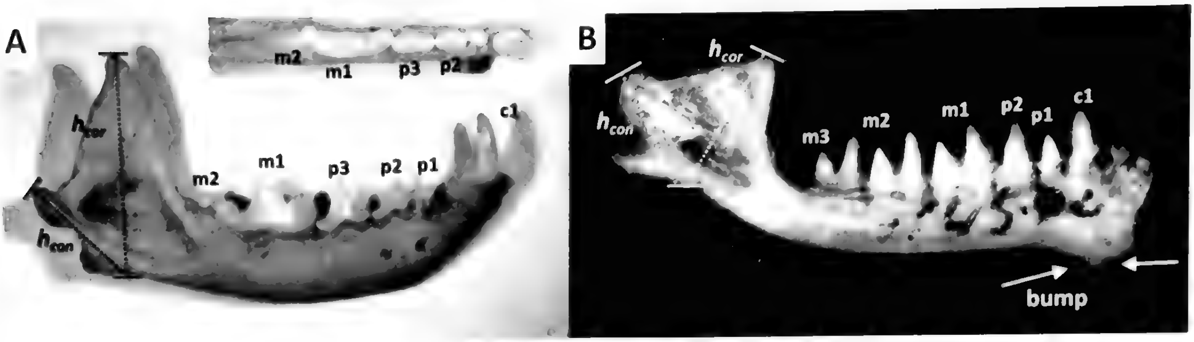

FIGURE 5. (*labial view*) Dentary bones of carnivores (*Mustela erminea*) (A) and chiropterans (*Perimyotis subflavus*) (B) with the height of the condyle (h_{con}), height of the coronoid process (h_{cor}), and the conspicuous mandibular bump of chiropterans.

complete absence of teeth on specimens of Cricetidae) may be generalized, the resistance of mandibles to degradation and the number of criteria we included in the key should prove useful in identifying lightly degraded mandibles to the species level.

Sex and age are important factors that may mean that certain mandible criteria may not be useful (because of sexual dimorphism and growth). We acknowledge that this may be a limitation to a key based on osteometry. Identifications conducted on bones of juveniles that are mixed with bones of adult prey may have a lower resolution (i.e., identifications stop at the genus level) than when only adults are present. As a solution, we included in the vast majority of couplets one or more known morphologic characters that are persistent through age and that do not differ between males and females, such as the morphology of the ramus. Using the mandible is also a useful tool for the counting of individual remains and do not necessitate lengthy and costly methods that often require advanced laboratory skills (e.g., identifications using DNA).

This is a new tool for identifying and monitoring all of the small mammals of eastern Canada. To our knowledge, this is the first comprehensive key designed in North America that uses the mandible exclusively. Use of the mandible enables degraded specimens of most small mammals to be identified down to the species level and it facilitates counting activities. Moreover, bats of the genera *Myotis*, *Perimyotis*, and *Eptesicus* have declined dramatically in the past few years as a result of the spread of white-nose syndrome (caused by *Pseudogymnoascus destructans*) in the eastern part of the United States and Canada (Blehert *et al.* 2009). Identifying mandibles on the floor of caves and in other hibernacula might be useful for monitoring carcasses.

Acknowledgements

Financial support was provided by the Natural Sciences and Engineering Research Council of Canada (NSERC) and the Fonds de recherche du Québec – Nature et technologies (FRQNT) of Quebec. We thank the Centre for Forest Research and the Conseil de recherches en sciences naturelles et en génie du Canada – Université du Québec en Abitibi-Témiscamingue–Université du Québec à Montréal (CRSNG-UQAT-UQAM) Industrial Chair in Sustainable Forest Management for technical support. We thank the Canadian Museum of Nature and Michel Gosselin and Kamal Khidas (both of the Canadian Museum of Nature) for their help with the skull collection and for providing us with a digital camera attached to a binocular. We thank David W. Nagorsen for providing constructive comments on earlier versions of the manuscript. We thank Amélie Drolet for linguistic revision of the text. We also thank all field assistants who participated in the collection of bones and the small mammal trapping campaigns.

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Supplementary material available at:
http://www.canadianfieldnaturalist.ca

Received 9 January 2013
Accepted 8 April 2013

Glossary of terms

Alveolus	Socket in which the roots of a tooth are set (Figures 24, 25, and 28) (*alv*).
Angular process	Posterior and ventral-most bony projection of the mandible; the angular process is posterior to the coronoid process (Figures 1 and 24) (*ang*).
Anteroconid	Anterior-most cusp on the m1 of jumping mice (Figure 19) (*antc*).
Anteromedian fold	Concave fold created by the anteroconid on the anterior part of m1 (*antf*).
Anteroposterior length	Length in the direction of the mandibular tooth row.
Brachydont tooth	Closed-rooted tooth with determinate growth (Figures 22 and 23).
Condyle/condylar process	Bony projection located on the ramus between the coronoid and the angular process (Figures 1 and 24) (*con*).
Coronoid process	Posterior and dorsal-most bony projection of the mandible; the coronoid process is anterior to the angular process (Figures 1 and 24) (*cor*).
Closed triangle (of enamel)	In rodents, the external layer of molars that forms occlusal triangular shapes (Figures 16 and 21) (*ct*).
Mandibular foramen	Small hole located below the temporal fossa and serves as a canal for the dental nerve.
Dentary bone	One side (half) of the mandible.
Diastema (plural: diastemata)	Space between two adjacent teeth (Figure 2) (*dia*).
Enamel	The hard external layer of the tooth.
Horizontal ramus	The anterior part of the dentary that supports the teeth (Figure 1B) (*hra*).
Hypoconid	The most posterior cusp (Figure 24).
Hypsodont tooth	Continually growing tooth. The enamel typically covers most of the tooth. Teeth are rootless (Figures 22 and 23).
Interdenticular space	Space between the cusps present on the incisors of shrews (Figure 30).
Labial	Next to the lips.
Labiolingual width	Length of teeth in the direction perpendicular to the mandibular tooth row.
Length of the mandibular tooth row	Length of the lower tooth row (c1–m3) (Figures 1, 6, 33, 37, and 42).
Lingual	Next to the tongue; the interior of the mouth.
Mandible	Both dentary bones, often referred as the lower jaw (*ma*).
Mandibular tooth row	All contiguous teeth of one dentary bone (*mt*). In Carnivora, Chiroptera, and Soricimorpha, all teeth form the toothrow. In Rodentia and Lagomorpha, premolars and molars form the toothrow.
Mental foramen	Small hole located on the labial face of the horizontal ramus (Figure 24).
Metaconid	Cusp posterior to the anteroconid on the lingual side of m1 in jumping mice.
Occlusal	The side of the teeth which meets with the opposing teeth.
Paraconid	Anterior-most cusp on molars in lateral view (Figure 24).
Pigmentation	Coloration of the teeth (*pg*). It is often dark in shrews.
Postmandibular foramen	Small hole next to the mandibular foramen that connects with the temporal fossa (Figure 30).
Premetaconid fold	Small depression, resembling a trench, separating the anteroconid from the metaconid on the molars of jumping mice (Figure 19) (*prmf*).
Protoconid	Middle cusp on the molars of shrews in lateral view (Figures 19 and 24).
Re-entrant angles	Inward pointing angle defined by the margin of the prismatic molars in voles (Figures 16 and 21) (*ra*).
Temporal fossa	Large opening on the lingual side of the vertical ramus.
Vertical ramus	The posterior part of the dentary, composed of the coronoid, condylar, and angular processes (Figure 1B) (*vra*).

Key to the mandibles of small mammals of eastern Canada

(full key illustrated with pictures provided in Supplementary material available at: http://www.canadianfield naturalist.ca)

A. General key to small mammals

1a. Wide diastema between the incisor and molars (Figure 2A) 2
1b. No diastema between the incisor and molars (Figure 2B) 3

2a. Two premolars and three molars; coronoid process and condylar process not differentiated or coronoid process minute (Figure 3A) .... Lagomorpha (section B) 5
2b. One premolar or none and three molars; coronoid process clearly differentiated from the condylar process (Figure 3B) .... Rodentia (section C) 7

3a. Canines and premolars similar in size; well-developed angular process that is often the most posterior part of the dentary bone (Figure 4A) .... Soricomorpha (section D) 31
3b. Canines two to three times the size of the adjacent premolar; small but robust angular process .... (Figure 4B) 4

4a. The most posterior molar often much smaller than the most anterior molar; lower edge of ramus without a bump under the canine; height of the coronoid process much higher than the height of the condylar process (Figure 5A) .... Carnivora (section E) 42
4b. Three W-shaped molars of similar size; lower edge of ramus with a bump under the canine; height of the coronoid process similar in size to or slightly higher than the height of the condylar process (Figure 5B) .... Chiroptera (section F) 50

B. Lagomorpha (Leporidae)

5a. Height of coronoid process >40 mm; length of mandibular tooth row >16 mm (Figure 6A) .... *Lepus arcticus*, *L. townsendii*, *L. europaeus*
5b. Height of coronoid process <40 mm; length of mandibular tooth row <16 mm (Figure 6B) 6

6a. Mental foramen easily visible from the occlusal view (Figure 7A) .... *Sylvilagus floridanus*
6b. Mental foramen barely visible from the occlusal view (Figure 7B) .... *Lepus americanus*

C. Rodentia (Cricetidae, Dipodidae, Erethizontidae, Muridae, and Sciuridae)

7a. Lower edge of horizontal ramus with sharp angle under p1 (Figure 8A); angular process clearly smaller than the coronoid process; cheek teeth with closed circular patterns of enamel (Figure 8B) .... *Erethizon dorsatum*
7b. Lower edge of horizontal ramus smooth; the coronoid process and the angular process are similar in size or the angular process is larger than the coronoid process; cheek teeth with triangular patterns of enamel or without clearly defined patterns 8

8a. Angular process clearly the most exterior part of the mandible (Figure 9A); angular process about twice as wide labially as the condylar process (Figure 9A); anterior edge of the coronoid process that connects with the angular process creates a bump pointing outwards at the level of p1-m1 in the occlusal view (Figure 9B); .... *Marmota monax*
8b. The condylar process or the coronoid process is the most exterior part of the mandible (occlusal view); no bumps created by the edge of the coronoid and angular processes next to p1-m1; angular process about the same labial thickness or less than the condylar process 9

9a. Tip of the angular process clearly higher than the teeth (Figure 10A) .... *Ondatra zibethicus*
9b. Tip of the angular process below or even with the teeth (Figure 10B) 10

10a. One premolar (Figure 11A); angular process extends slightly behind the coronoid process (Figure 11C) 11
10b. No premolar (Figure 11B); angular process extends well behind the coronoid process (Figure 11D) 18

11a. Coronoid process long; size of the notch between the coronoid and condylar processes similar in size to the notch between the condylar and angular processes (Figures 12A and 12B) 12
11b. Coronoid process relatively short; size of the notch between the coronoid and condylar processes clearly smaller than the notch between the condylar and angular processes (Figures 12C and 12D) . . 14

12a. T-shaped condylar process; angular and condylar processes equally posterior (Figure 12A) . . . . *Poliocitellus franklinii*
12b. A-shaped condylar process; condylar process clearly the most posterior component of the ramus (Figure 12B) 13

13a. Length of the mandibular tooth row <5.5 mm . . . . *Tamias minimus*
13b. Length of the mandibular toothrow >5.5 mm . . . . *Tamias striatus*

14a. Height of the coronoid process >17 mm; length of the mandibular tooth row >35 mm 15
14b. Height of the coronoid process <17 mm; length of the mandibular tooth row <35 mm 16

15a. Coronoid process short; notch created by the coronoid process and the condylar process appears wide open; lower tip of the angular process appears squared (Figure 13A) . . . . *Sciurus niger*
15b. Coronoid process longer; coronoid notch narrow; lower tip of the angular process appears rounded (Figure 13B) . . . . *Sciurus carolinensis*

16a. Uppermost edge of the condylar process relatively flat (Figure 14A) . . . . *Tamiasciurus hudsonicus*
16b. Uppermost edge of the condylar process concave (Figure 14B) 17

17a. Posterior tip of the angular process above the notch on the lower edge of the horizontal ramus (Figure 15A) . . . . *Glaucomys volans*
17b. Posterior tip of the angular process below or at the same level as the notch on the lower edge of the horizontal ramus (Figure 15B) . . . . *Glaucomys sabrinus*

18a. Molars without re-entrant angles or closed triangles (Figure 16A) 19
18b. Molars with well-defined lingual and labial re-entrant angles (Figure 16B), often with closed triangles of enamel (Figure 16C) 23

19a. Condylar process clearly the most posterior part of the dentary bone; coronoid process small, at about the same height as the condylar process (Figure 17A) . . . . *Peromyscus leucopus* or *P. maniculatus*
19b. Condylar process slightly posterior to the angular process or about equally posterior; coronoid process relatively long and higher than the condylar process (Figure 17B) 20

20a. Molars with complex patterns of enamel loops (Figure 18A) 21
20b. Molars with simple patterns of enamel loops (Figures 18B and 18C) 22

21a. Anteromedian fold present on m1; anteroconid of m1 clearly separated from the protoconid by the preprotoconid and premetaconid folds (Figure 19A) . . . . *Zapus hudsonius*
21b. Anteromedian fold absent on m1; anteroconid of m1 not separated or slightly separated from the protoconid by the premetaconid fold (Figure 19B) . . . . *Napaeozapus insignis*

22a. Molars with simple patterns of enamel (Figure 20A) . . . . *Mus musculus*
22b. Molars with two rows of cusps without patterns of enamel (Figure 20B) . . . . *Rattus norvegicus*

23a. Re-entrant angles of molars much deeper on lingual side than on labial side (Figures 21A, 21B, and 21C) 24
23b. Re-entrant angles of molars equal in size on both lingual and labial side (Figures 21D, 21E, 21F, 21G, 21H, and 21I) 26

24a. Brachydont teeth (molars closed-rooted) (Figures 22A, 22B, 22C, 23A, and 23B); several small closed triangles on the labial side of molars (Figure 21A) . . . . *Phenacomys ungava*
24b. Hypsodont teeth (molars open-rooted) (Figures 22D and 23C); one closed triangle or none on the labial side of each molar (Figures 21B and 21C) 25

25a. A single closed triangle on the labial side of each molar (Figure 21B) .... *Synaptomys cooperi*
25b. No closed triangle on the labial side of molars (Figure 21C) .... *Synaptomys borealis*

26a. Brachydont teeth (molars closed-rooted) (Figures 22A, 22B, 22C, 23A, and 23B); occlusal triangles of molars rounded and "enclosed" by the enamel borders (Figures 21D and 21E) 27
26b. Hypsodont teeth (molars open-rooted) (Figures 22D and 23C); occlusal closed triangles with sharp tips (Figures 21F, 21G, 21H, and 21I) 28

27a. Occlusal triangular shapes of enamel of m1 and m2 often connected by wide bridges; shape of the anterior triangle of m3 is typically similar to the posterior triangles (Figure 21D) .... *Myodes gapperi*
27b. Occlusal triangles on m1 and m2 often connected by narrow bridges; shape of the anterior triangle of m3 often different from the other triangles (Figure 21E) .... *Myodes glareolus*

28a. Presence of a small fold of enamel on the anterior and lingual side of m2 (Figure 21F) .... *Dicrostonyx hudsonius*
28b. Absence of a small fold of enamel on the anterior and lingual side of m2 (Figures 21G, 21H, and 21I) 29

29a. Three closed triangles on m1 (Figure 21G) .... *Microtus pinetorum*
29b. Five closed triangles on m1 (Figures 21H and 21I) 30

30a. Two closed triangles on m2 (Figure 21H) .... *Microtus chrotorrhinus*
30b. Four closed triangles on m2 (Figure 21I) .... *Microtus pennsylvanicus*

D. Soricomorpha (Soricidae and Talpidae)

31a. Teeth all white; incisors without a posterior cusp; alveolus of incisors does not extend under premolars or molars (Figure 25A) 32
31b. Tip of teeth often with red and/or brown pigments; incisors with a posterior cusp; alveolus of incisors extends beneath the first premolar or posteriorly (Figures 24 and 25B) 34

32a. Two incisors, no canine, and three premolars; presence of a short diastema between the second incisor and the first premolar (Figure 26A) .... *Scalopus aquaticus*
32b. Three incisors, one canine, and four premolars; presence of several short diastemata between the premolars (Figure 26B) or complete absence of diastemata (Figure 26C) 33

33a. Canine and the first three premolars separated by short diastemata; angular process long and slender; condylar process about the same height as the coronoid process or higher; coronoid process clearly smaller than the condylar process (Figure 26B) .... *Condylura cristata*
33b. Canine and first three premolars not separated by diastemata; coronoid process higher than the condylar process; coronoid larger than the condylar process (Figure 26C) .... *Parascalops breweri*

34a. Alveolus of incisor extends slightly or substantially beneath m1; alveolus extends at the level of the m1 paraconid or posteriorly (Figure 27A) 35
34b. Alveolus of incisor does not extend beneath the m1 paraconid (Figure 27B) 36

35b. Three small cusps on the occlusal surface of the incisor; angular process long and very slender (Figure 28A) .... *Sorex hoyi*
35a. One or two small cusps on the occlusal surface of the incisor; angular process relatively short and robust (Figure 28B) .... *Blarina brevicauda*

36a. Mental foramen located beneath the m1 paraconid; the space between both cusps on the molars is relatively large (Figure 29A) .... *Sorex dispar*
36b. Mental foramen located beneath the m1 protoconid or posteriorely; the space between both cusps on the molars is relatively small (Figure 29B) 37

37a. Postmandibular foramen present (Figure 30A); deep interdenticular spaces on i1 (Figure 30B) ... 38
37b. Postmandibular foramen absent; shallow interdenticular spaces on i1 (Figure 30C) 39

38a. Height of coronoid process <4.5 mm (Figure 24) . . . . *Sorex maritimensis*
38b. Height of coronoid process >4.5 mm (Figure 24) . . . . *Sorex arcticus*

39a. Height of coronoid process >4.5 mm (Figure 24) . . . . *Sorex palustris*
39b. Height of coronoid process <4.5 mm (Figure 24) 40

40a. Height of coronoid process <3.75 mm (Figure 24) . . . . *Sorex cinereus*
40b. Height of coronoid process >3.75 mm (Figure 24) . . . . *Sorex fumeus*

E. Carnivora (Canidae, Mephitidae, and Mustelidae)

41a. Two molars; very small to no diastema between c1 and p1; anterior part of the ramus under the canine thick (Figure 31A) 42
41b. Three molars; diastema between c1 and p1 about equal in size to p1 or larger; anterior part of the ramus under the canine slender (Figure 31B) 48

42a. Four premolars (Figure 31A) 43
42b. Three premolars (Figure 32) 44

43a. Length of the mandibular tooth row <38 mm; posterior mental foramen located beneath the hypoconid of p3; coronoid process relatively sharp (Figure 33A) . . . . *Martes americana*
43b. Length of the mandibular tooth row >38 mm; posterior mental foramen often located beneath the protoconid of p3; coronoid process rounded (Figure 33B) . . . . *Martes pennanti*

44a. Bump present on the anterior part of the horizontal ramus approximately beneath p1 (Figure 34A); p1 clearly smaller than m2 (Figure 34C) . . . . *Mephitis mephitis*
44b. Absence of a bump on the anterior part of the horizontal ramus (Figure 34B); p1 larger than m2 or about similar in size (Figure 34D) 45

45a. p2 often with a well-developed paraconid (Figure 35A); posterior edge of the vertical ramus with a distinct convex notch between the coronoid process and the condylar process (Figure 36A) . . . . *Neovison vison*
45b. p2 often without a small anterior cusp (Figure 35B); posterior edge of the vertical ramus straight between the coronoid process and the condylar process (Figure 36B) 46

46a. Height of coronoid process <7.1 mm; length of mandibular tooth row <10 mm (Figure 37) . . . . *Mustela nivalis*
46b. Height of coronoid process >7.1 mm; length of mandibular tooth row >10 mm (Figure 37) 47

47a. Height of the coronoid process generally <10.5 mm; length of mandibular tooth row never >16 mm (Figure 37); posterior edge of the vertical ramus between the coronoid process and the condylar process relatively flat (Figure 38A) . . . . *Mustela erminea*
47b. Height of the coronoid process generally >10.5 mm; length of mandibular tooth row often >16 mm (Figure 37); posterior edge of the vertical ramus between the coronoid process and the condylar process with a convex curve (Figure 38B) . . . . *Mustela frenata*

48a. Presence of a clearly defined step on the lower edge of the horizontal ramus anterior to the angular process; diastemata between c1 and p1, between p1 and p2, and between p2 and p3 (Figure 39A) . . . . *Urocyon cinereoargenteus*
48b. Lower edge of the horizontal ramus anterior to the angular process smooth, without a step; only one diastema between c1 and p1 (Figure 39B) 49

49a. Anteroposterior length of the diastema between c1 and p1 smaller than p1 (Figure 40A) . . . *Vulpes lagopus*
49b. Anteroposterior length of the diastema between c1 and p1 about equal to p1 or larger (Figure 40B) . . . . *Vulpes vulpes*

F. Chiroptera (Vespertilionidae)

50a. Three premolars (Figure 41A) 51
50b. Two premolars (Figure 41B) 54

51a. Mandibular length >11.5 mm (Figure 42); hypoconid of p3 with lingual crest directed medially creating a distinct lingual bulge (Figure 43A) . . . . *Lasionycteris noctivagans*
51b. Mandibular length <11.5 mm (Figure 42); hypoconid of p3 without a distinct lingual bulge (Figure 43B) 52

52a. p3 rectangular, anteroposterior length greater than labiolingual width (Figure 44A); mandibular length generally ≥11mm (Figure 42) . . . . *Myotis septentrionalis*
52b. p3 squared, anteroposterior length approximately equal to labiolingual width (Figure 44B); mandibular length <11mm (Figure 42) 53

53a. Mandibular length generally >10 mm; length of the mandibular tooth row generally >5.5 mm (Figure 42) . . . . *Myotis lucifugus*
53b. Mandibular length generally <10 mm; length of the mandibular tooth row generally <5.5 mm (Figure 42) . . . . *Myotis leibii*

54a. Mandibular length >12.5 mm (Figure 42) 55
54b. Mandibular length <12.5 mm (Figure 42) 56

55a. Mandibular length >14 mm (Figure 42); rounded coronoid process much taller than c1 (Figure 45A); p2 squared, with labiolingual width approximately equal to anteroposterior length (Figure 46A) . . . . *Eptesicus fuscus*
55b. Mandibular length ≤14 mm (Figure 42); sharp coronoid process approximately same height as c1 (Figure 45B); p2 rectangular with labiolingual width greater than anteroposterior length (Figure 46B) . . . . *Lasiurus cinereus*

56a. Length of the mandibular tooth row <5 mm (Figure 42); small diastemata separate i2 from i3, i3 from c1, and p1 from p2; c1 approximately same height as p2 (Figure 47A) . . . . *Perimyotis subflavus*
56b. Length of the mandibular tooth row >5 mm (Figure 42); no diastema between i2 and i3, i3 and c1, or p1 and p2; c1 taller than p2 (Figure 47B) . . . . *Lasiurus borealis*

Characteristics of Barred Owl (*Strix varia*) Nest Sites in Manitoba, Canada

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Whiklo, Todd M., and James R. Duncan. 2014. Characteristics of Barred Owl (*Strix varia*) nest sites in Manitoba, Canada. Canadian Field-Naturalist 128(1): 38–43.

During 2009 and 2010, nine Barred Owl (*Strix varia*) nest sites were located in Manitoba, Canada, and data on nest trees, nest structure, and nest site habitat were collected. Nests were located in a variety of tree species, including Balsam Poplar (*Populus balsamifera*), Paper Birch (*Betula papyrifera*), Trembling Aspen (*Populus tremuloides*) and Burr Oak (*Quercus macrocarpa*). All nests were in tree cavities, and the majority of nests were in dead trees (67%) and had lateral openings (67%). Habitat surrounding nest trees and estimated canopy cover were highly variable. Diameter at breast height of nest trees, cavity width, and cavity depth were consistent and were determined to be the most reliable indicators of nest suitability for breeding Barred Owls. We conclude that the distribution of nesting Barred Owls is influenced more by availability of suitable nest sites than by nest tree species or nest site habitat.

Key Words: Barred Owl; *Strix varia*; habitat; nesting; raptor; Manitoba

Introduction

Barred Owls (*Strix varia*) nest in a variety of natural and anthropogenic structures (Robertson 1959; Shackleford 1996; Houston 1999), but are considered to be primarily cavity nesters (Mazur *et al.* 1997a, 1997b). They use tree cavities created by other birds, disease, rot, and/or tree damage (Mazur *et al.* 1997a; Vaillancourt *et al.* 2009). Because of its reliance on large diameter trees for nesting, the Barred Owl is considered an indicator species of forest health (McGarigal and Fraser 1984). The availability of nest sites limits its distribution, population size, and density (Robertson and Rendell 1990).

As a highly adaptable species (Robertson 1959; Shackleford 1996), the Barred Owl persists in some habitats that have been altered by human activity (Kelly *et al.* 2003; Houston 1999). However, nesting requirements must be met in order for avian populations to be maintained (Robertson and Rendell 1990). The Barred Owl's nesting requirements are poorly documented throughout most of its range (North America) (Mazur *et al.* 1997a), and specifically in Manitoba (Holland *et al.* 2003).

Across its range, the Barred Owl uses forest types along a gradient from hardwood to mixedwood to softwood forests (Nicholls and Warner 1972). Hardwood forests are rare throughout a large portion of its northern range, leaving only mixedwood and mostly boreal forests (Duncan and Kearns 1997). The link between large cavity-nesting species and mature stands of mixedwood forests is known (McGarigal and Fraser 1984; Potvin *et al.* 2000; Hodson 2003; Payer and Harrison 2003).

Barred Owl management and conservation by the government in Manitoba and elsewhere will be more effective if we understand which factors create suitable Barred Owl habitat within various mature mixedwood stands. Our objectives were to locate Barred Owl nest sites in Manitoba, Canada, and collect data on nests, nest trees, and nest site habitat. Describing these factors will contribute to hypotheses about nest and habitat selection in this species and the limits to their distribution in Manitoba and elsewhere.

Study Area

Research was conducted from February 2009 to September 2010 within the southern portion of Manitoba, Canada (49°0.0'N to 53°52.7'N and 95°9.2'W to 101°44.2'W). This area consists of prairie pothole, boreal hardwood transition, boreal taiga plain, and boreal softwood shield regions (Zoladeski *et al.* 1995). Predominant tree species in the study area were White Spruce (*Picea glauca*), Black Spruce (*Picea marinana*), Tamarack (*Larix laricina*), Jack Pine (*Pinus banksiana*), Trembling Aspen (*Populus tremuloides*), Balsam Poplar (*P. balsamifera*), and Paper Birch (*Betula papyrifera*). Southern Manitoba lacks major topographic changes; however, small shifts in elevation, along with the abundance of wetlands and waterways, create a highly variable habitat (Zoladeski *et al.* 1995).

Methods

Barred Owl nest sites were located using nocturnal audio surveying and diurnal audio playback with passive observation during the breeding season (February – June in 2009 and 2010) (Frith *et al.* 1997; Whiklo 2011). Survey transects were laid out in areas based on Barred Owl detection data obtained from the Manitoba Nocturnal Owl Survey (JRD, unpublished data; *op. cit.* Duncan and Kearns 1997) and historical accounts, and

transects were also laid out in suitable habitat adjacent to known areas of Barred Owl activity. In total approximately 1321 km of transect lines were surveyed in 2009 and 2010. Survey locations were situated 1.6 km apart along survey transects where playback of Barred Owl vocalizations were used to elicit responses (Whiklo 2011). Areas where Barred Owls were detected during nocturnal surveys were searched during daylight for active nests.

Nest trees were categorized as live or dead, and tree species, the height of the nest above ground, and diameter at breast height (DBH) were recorded. Diameter at breast height was calculated by measuring the circumference of the tree and then calculating the diameter: $D = C/\pi$. Cavity height (distance from the lowest point inside the nest to the highest point inside the nest), cavity width (distance from the furthest right-hand point inside the cavity to the furthest left-hand point inside the cavity), and cavity depth (distance inside the cavity perpendicular to cavity width) were measured; nest type (cavity, stick, other) and cavity orientation (lateral or apical) were also recorded.

Habitat within a 30 m circular plot surrounding the nest trees was categorized using Manitoba Forest Inventory classifications (Zoladeski *et al.* 1995), and the percentage canopy cover was estimated (Whiklo 2011). All measurements are reported as mean and standard deviation (SD).

Results

A total of nine Barred Owl nests were located in 2009 and 2010 within a 25 000 km^2 rectangle in southeastern Manitoba. All nests were cavity type structures; six were lateral cavities and three were apical cavities (Table 1). Six nest trees were dead and three were living (Table 1). Five nests were found in Balsam Poplar, two in Paper Birch, one in Trembling Aspen, and one in Burr Oak (Table 1). The mean nest height above ground was 7.7 m (SD 2.6). The mean diameter at breast height of nest trees was 49.2 cm (SD 18.9). The mean cavity height was 71.8 cm (SD 46.9), the mean cavity depth was 42.1 cm (SD 33.0), and the mean cavity width was 27.3 cm (SD 5.4) (Table 2).

Four nest trees were located in Balsam Poplar mixedwood (V1) stands, two in Black Ash (*Fraxinus nigra*) hardwood (V2) stands, one in a White Spruce/Balsam Fir (*Abies balsamea*) (V21) stand, one in a Miscellaneous Hardwood (V3) stand, and one in an area that could not be classified due to a lack of living trees (a pond created by an American Beaver, *Castor canadensis*) (Table 1). The mean estimated canopy cover was 42.8% (SD 27.2) (Table 2).

Discussion

There are a considerable number of studies that examine one or more aspects of the nest site structure, the nest tree species, and/or the habitat associated with the nest sites of the Barred Owl (Nicholls and Warner 1972;

TABLE 1. Data for nine Barred Owl (*Strix varia*) nest sites in Manitoba, Canada (2009 to 2010).

Owl nest site	Nest tree species	Nest tree status	Nest type	Manitoba forest classification[1]
Cow Moose Lake (Barred Owl 4)	Balsam Poplar	Dead	Lateral cavity	V1: Balsam poplar hardwood and mixedwood
Watson P. Davidson Wildlife Management Area (Barred Owl 5)	Paper Birch	Dead	Apical cavity	V1: Balsam poplar hardwood and mixedwood
Stead (Barred Owl 11)	Balsam Poplar	Dead	Lateral cavity	V1: Balsam poplar hardwood and mixedwood
Otter Falls (Barred Owl 20)	Balsam Poplar	Dead	Lateral cavity	NA*
Nutimik Lake (Barred Owl 27)	Balsam Poplar	Live	Lateral cavity	V2: Black ash (White elm) hardwood
West of Woodridge (Barred Owl 31)	Balsam Poplar	Dead	Apical cavity	V21: White spruce Balsam fir shrub
East of Piney (Barred Owl 36)	Paper Birch	Dead	Apical cavity	V1: Balsam poplar hardwood and mixedwood
Contour area (Barred Owl 55)	Trembling Aspen	Live	Lateral cavity	V2: Black ash (White elm) hardwood
Dencross (Barred Owl 56)	Burr Oak	Live	Lateral cavity	V3: Miscellaneous hardwoods

*Habitat was determined to be unclassifiable according to Manitoba forest classifications due to lack of living trees.
[1] Zolandeski *et al.* (1995)

TABLE 2. Further data for nine Barred Owl (*Strix varia*) nest sites in Manitoba, Canada (2009 to 2010).

Owl nest site	Nest tree diameter at breast height (cm)	Height of the nest above the ground (m)	Cavity height (cm)	Cavity depth (cm)	Cavity width (cm)	Canopy cover (%)
Cow Moose Lake (Barred Owl 4)	43.1	4.5	68.8	26.4	27.8	30
Watson P. Davidson Wildlife Management Area (Barred Owl 5)	42.9	7.4	24.9	32.9	29.4	35
Stead (Barred Owl 11)	50	10.2	156.0	127.0	24.5	60
Otter Falls (Barred Owl 20)	39.7	6.4	121.1	22.8	26.1	0
Nutimik Lake (Barred Owl 27)	56.2	12.1	67.9	35.9	35.9	70
West of Woodridge (Barred Owl 31)	33.7	5.8	11.4	22.3	21.5	75
East of Piney (Barred Owl 36)	33.3	5.4	42.0	29.8	21.2	5
Contour area (Barred Owl 55)	48.7	7.6	102.2	30.8	35.1	50
Dencross (Barred Owl 56)	95.5	9.9	52.2	51.0	24.0	60
Mean (SD)	49.2 (18.9)	7.7 (2.6)	71.8 (46.9)	42.1 (33.0)	27.3 (5.4)	42.8 (27.2)

Haney 1997; Mazur *et al.* 1997a, 1997b; Postupalsky *et al.* 1997; Winton and Leslie 2004; Olsen *et al.* 2006; Grossman *et al.* 2008; Singleton *et al.* 2010) and general Barred Owl habitat associations (McGarigal and Fraser 1984; Booth and Harrison 1997; Mazur *et al.* 1998; Hamer *et al.* 2007; Russell 2008). These studies vary considerably, as described in more detail below, in the way study areas were selected, in the size and habitat fragmentation of the study areas, and in the size and measurement of nest habitat plots. However, there is less variation in the way nest trees and nest sites were measured.

This variation in methodology limited our ability to compare results; nevertheless, some Barred Owl nest site characteristics were consistent across studies.

Nest type

In contrast to other studies (Mazur *et al.* 1997a; Postupalsky *et al.* 1997; Olsen *et al.* 2006), all nests ($n = 9$) located in the study were in tree cavities (Table 1). Mazur *et al.* (1997a) reported that 5 of 15 Barred Owl nests (33%) in the study in the boreal forest of Saskatchewan were in structures other than tree cavities; in witch's broom (the dense branching caused by *Arceuthobium* spp. in a White Spruce tree), in Red Squirrel (*Tamiasciurus hudsonicus*) nests, or in stick nests. In a study in the boreal mixedwood forest in Alberta (Olsen *et al.* 2006), 9 of 10 nest sites (90%) were in tree cavities (one Barred Owl nested in a stick nest). In Michigan, in hardwood (deciduous) and mixed forest habitat, Postupalsky *et al.* (1997) described 13 of 57 nests (23%) as being open sites, including hawk (Red-shouldered Hawk (*Buteo lineatus*) or Broad-winged Hawk (*Buteo platypterus*) and Northern Goshawk (*Accipiter gentilis*)) stick nests, a ground nest, a flat area in the fork of a Yellow Birch (*Betula alleghaniensis*), and a nest platform intended for Great Horned Owls (*Bubo virginianus*); the remainder were in tree cavities ($n = 26$) or nest boxes ($n = 18$).

The likelihood of finding an open Barred Owl nest in Manitoba would presumably increase with increased effort and sample size. However, it is noteworthy that, even though Barred Owls are known to use artificial open nests (Olsen *et al.* 2006), none were found nesting on a cumulative total of 2527 natural and/or artificial open stick platform nests in a variety of habitats checked for raptors over a 27-year period (1984–2010) in the same 25 000 km^2 study area in southeastern Manitoba (Duncan 1992; JRD, unpublished data).

The aforementioned studies (Mazur *et al.* (1997a), Postupalsky *et al.* (1997), and Olsen *et al.* (2006)) varied considerably in the way the study areas were selected or described, in the size of the study areas, in the methods used to find nests, in the forest habitat composition/fragmentation, and in other quantified ways (i.e., prey density, human disturbance). For example, this study was larger (~25 000 km^2) with varied habitat, the study described in Mazur *et al.* (1997a) was conducted within a 3 874 km^2 national park, the study described in Olsen *et al.* (2006) was a 800 km^2 predetermined area, and two study areas (28 km^2 and an undefined larger area) were studied in Postupalsky *et al.* (1997).

Smaller fragmented study areas or isolated protected areas (i.e., national parks) may vary in terms of the availability of cavity nests, the prey density, the forest habitat, and/or intra and interspecific competition, resulting in the variation observed in the proportion of nest type use by breeding Barred Owls. How these factors affect the availability of suitable cavity nest sites and the proportion of Barred Owls using open nest sites is unknown. However, the propensity of Barred Owls for cavity nests likely results from natural selection; Barred Owls nesting in cavities experience greater reproductive success than those that use open nests (Postupalsky *et al.* 1997).

Nest cavity characteristics

Given the importance of nest cavities to Barred Owl reproduction, we recorded a series of measurements. Cavity height and depth ranged widely (height ranged

from 11.4 to 156.0 cm and depth ranged from 22.3 to 127.0 cm) with high standard deviations, whereas cavity width was remarkably consistent (21.2 to 35.9 cm) (Table 2), despite the variation in nest tree species and status (live or dead) (Table 1). Cavity depth varied the most, perhaps as a result of the variable and sometimes advanced stages of tree decay, e.g., the nest site near Stead (Table 2). Postupalsky *et al.* (1997) recorded a similar mean cavity width (26.9 cm, range 18–44, $n = 25$), but did not report cavity depth measurements (as defined in this study) or standard deviations. Nest cavity measurements were not reported in other studies.

Nest tree diameter at breast height

Mean diameter at breast height of nest trees in this study (49.2 cm, SD 18.9) was consistent with that reported in other studies. Mazur *et al.* (1997a) recorded an average diameter at breast height of 47.4 cm (SD 12.8, $n = 15$), despite recording considerably higher values for the height of nests from the ground (13.3 m, SD 4.1) than this study (7.7 m, SD 2.6) (Table 2). Olsen *et al.* (2006) recorded an average diameter at breast height of 51.6 cm (SE 4.3), along with a relatively intermediate nest height above ground (10.4 m, SE 2.1).

There were relatively large differences in many nest tree variables among these studies (e.g., nest tree height, nest height, proportion of cavity nest structures, and nest tree species); therefore, the similarities in the diameter at breast height of nest trees suggest it is a valid and practical indicator of Barred Owl nest tree suitability.

Nest tree species, percentage canopy cover, and forest stand composition

Barred Owls nested in four hardwood tree species in this study (Table 1), and this variation was similar to that found in other studies. Mazur *et al.* (1997a) reported Barred Owl nests in both softwood (coniferous) and hardwood tree species, including White Spruce ($n = 5$), Trembling Aspen ($n = 5$), Balsam Poplar ($n = 4$), and Paper Birch ($n = 1$). Olsen *et al.* (2006) documented Barred Owl nests in fewer tree species in a smaller study area: Balsam Poplar ($n = 8$) and Trembling Aspen ($n = 2$). Barred Owls use a variety of nest tree species, live or dead, and they readily breed in artificial nest boxes placed in a variety of trees (Postupalsky *et al.* 1997). It is therefore unlikely that Barred Owls choose a nest site based on tree species per se.

High percentage forest canopy cover has been cited as a determining factor in Barred Owl selection of breeding habitat, possibly because it provides solar insulation (Nicholls and Warner 1972; Haney 1997; Winton and Leslie 2004; Grossman *et al.* 2008), but the influence of forest canopy may depend on the size of the area that was measured. In this study, canopy cover was measured within a 30 m circular plot centered on the nest tree, and it did not appear to influence Barred Owl nest tree habitat use: more than half the sample had a canopy cover of ≤50% (Table 2).

Mazur *et al.* (1997b) used a similar small-scale plot (11.3 m radius) with the nest tree at the centre, and reported a somewhat higher mean percentage cover of 57% (SD 17); this was not significantly different from random plots. Other studies reported yet higher percentage canopy cover within larger Barred Owl home ranges: 96% (SE 1.1) (Haney 1997), 62.8% (Winton and Leslie 2004), utilized "dense" cover disproportionately (no values given) (Nicholls and Warner 1972), >66% (Grossman *et al.* 2008), and >56% (Singleton *et al.* 2010).

Forest stands within the 30 m circular plots (centered on nest trees) were classified as one of three types of stands: hardwood and mixedwood, softwood shrub, or unclassified (American Beaver pond) (Table 1). This variation in nest habitat use is reflective of the great variety of forested areas over the considerable North and Central American range of the Barred Owl, from swamps and riparian areas to upland regions (Mazur and James 2000). This variation of forest stand nesting habitat use suggests that the Barred Owl is a forest habitat generalist.

Management of forests for Barred Owls

Strong selective pressure on Barred Owls appears to have resulted in their propensity for nest cavities in trees. Observed higher reproductive success in cavity nests implies nest site selection for cavities by this species (Postupalsky *et al.* 1997). This conclusion is supported both by our results and by those of others, in which the most consistent nest characteristics and nest habitat characteristics reported are the width of the nesting cavity and the diameter at breast height of the nest tree. Other Barred Owl nest habitat characteristics discussed herein vary considerably across the range of the Barred Owl. Apart from its effective dependence on suitable nest tree cavities, the Barred Owl is otherwise generally considered a forest habitat generalist (Mazur and James 2000).

The persistence of Barred Owl populations depends on the maintenance of forests with trees with a minimum diameter at breast height capable of producing cavities large enough for this large cavity-nesting species (Haney 1997). Knowledge of ecological factors and processes that promote the formation of suitable nest tree cavities is also critical to the maintenance of Barred Owls in a managed forest environment.

Barred Owls are associated with water (Mazur *et al.* 1997b; Hamer *et al.* 2007), mature or "old-growth" forest stands (McGarigal and Fraser 1984; Mazur *et al.* 1998), and mixedwood or hardwood stands (Booth and Harrison 1997; Mazur *et al.* 1997b; Russell 2008).

The role and importance of heart rot in hardwood species in the formation of nest cavities, as well as the role of snags in an ecosystem, are well documented (Thomas *et al.* 1979; Witt 2010). Barred Owl nest cavities found in this study were natural and had resulted from damage to and decay of the tree. These cavities

were not readily attributable to excavation by primary cavity nesters.

Cavities not created by primary cavity nesters are often created by tree decay and rot (Bunnell *et al.* 2002). Fungal rot is prevalent in older and/or larger stands of trees (Witt 2010) and has positive effects for both primary and secondary cavity nesters (Bunnell *et al.* 2002). Higher levels of moisture and humidity, factors found at sites within close proximity to water, increase the rate of decay in trees (Jackson and Jackson 2004). In Manitoba, hardwood species decay at a higher rate than most softwood species: annual losses of hardwood species to decay are double that of softwood species (Brandt 1995).

Barred Owl conservation would benefit from the development and use of a standard methodology to characterize nest sites and nesting habitat. Standard methodology would allow the results from studies across this species' range or through time to be compared. We also recommend that tree species composition, diameter at breast height, and ecological forest decay indicators be developed and used to identify priority Barred Owl habitat conservation areas where forest habitat loss affects the viability of local Barred Owl populations.

Acknowledgements

This research was supported by Manitoba Conservation, Manitoba Hydro, the University of Manitoba, the Manitoba Model Forest Inc., the Raptor Research Foundation, and the Winnipeg Foundation. Thanks to Robert Nero and Terry Galloway for reviewing drafts of this manuscript and providing comments. We also thank the two anonymous reviewers for their helpful comments.

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Received 15 March 2013
Accepted 29 May 2013

Yellow Warblers (*Setophaga petechia*) Rear Second Broods in Some Years at Delta Marsh, Manitoba

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Sealy, Spencer G. 2014. Yellow Warblers (*Setophaga petechia*) rear second broods in some years at Delta Marsh, Manitoba. Canadian Field-Naturalist 128(1): 44–49.

Twenty cases of double brooding by colour-marked Yellow Warblers (*Setophaga petechia*) were recorded in 5 of 11 years (1975–1986, no data collected in 1977) during studies of breeding ecology in the dune-ridge forest at Delta Marsh, Manitoba (1 pair in 1975, 3 pairs in 1976, 3 pairs in 1984, 9 pairs in 1985, and 4 pairs in 1986). At least one member of each of the 20 pairs was marked. Eleven pairs re-used their first nest for the second attempt, whereas 9 females built a new nest, in 5 cases because the original nests had disintegrated. Four of the second nests (3 in 1985 and 1 in 1986) were parasitized by Brown-headed Cowbirds (*Molothrus ater*). All 20 first nests produced at least one young, a condition for double brooding, and 13 second nests, including 3 that were parasitized, were successful. Failure of about 60% of annual nesting attempts at Delta Marsh may contribute to the low number of pairs with double broods recorded in some years and the absence of double brooding in years of comparable phenology. This is the first published evidence of double brooding in the Yellow Warbler.

Key Words: double broods; Yellow Warbler; *Setophaga petechia*; Delta Marsh; Manitoba

Introduction

Knowledge of the number and success of broods attempted by birds in each breeding season is important for an understanding of the dynamics of avian populations and life history evolution (Martin 1987). One of the components of the life cycle is the number of broods individuals typically rear in each breeding season, whether one, two or even more in certain years when conditions are suitable. This contrasts with the replacement of clutches and broods that may be depredated or otherwise fail, possibly due to inclement weather.

An irrefutable determination that birds have raised one brood and attempted to raise another requires careful monitoring of colour-marked individuals or radio-tracking throughout the entire breeding season. In some species, researchers have recorded double brooding infrequently, often as isolated cases (e.g., in the Northern Yellow-throat, *Geothlypis trichas* (Stewart 1953); in Kirtland's Warbler, *Setophaga kirtlandii* (Radabaugh 1971); in the Bobolink, *Dolichonyx oryzivorus* (Gavin 1984); and in the Dickcissel, *Spiza americana* (Bolinger and Maddox 2000)), whereas others have recorded double brooding by 6–48% of pairs, with successful second broods increasing an individual's annual productivity (e.g., in the Black-throated Blue Warbler, *Setophaga caerulescens* (Holmes *et al.* 1992); in the Hooded Warbler, *Setophaga citrina* (Evans Ogden and Stutchbury 1996); and in the Louisiana Waterthrush, *Parkesia motacilla* (Mulvihill *et al.* 2009)).

During an 11-year study of breeding and feeding ecology of Yellow Warblers (*Setophaga petechia*) in a riparian habitat at Delta Marsh, Manitoba, from 1975 to 1986 (no data were collected in 1977), co-workers and I recorded irrefutable evidence of the rearing of second broods after young had fledged from first nests, but only in some years. Other workers have suspected double brooding by Yellow Warblers, but their observations were based on one or only a few nests attended by unmarked birds (e.g., Stoner 1932; Salt 1973; Bancroft 1979). Confirmation of double brooding by Yellow Warblers at the northern latitude of Delta Marsh suggests that double brooding may be a regular occurrence in this species' breeding biology.

Study Area

Data from first and second broods of the Yellow Warbler were recorded from nests discovered in the dune-ridge forest that separates Lake Manitoba and Delta Marsh, Manitoba, 50°11'N, 98°19'W (Goossen and Sealy 1982; MacKenzie 1982; MacKenzie *et al.* 1982; Pohajdak 1988). Nests were monitored over 11 years (1975–1986, except 1977) by J. P. Goossen (1975 and 1976) and by me in the other years, although some nests in the latter years were located by co-workers conducting other studies. The number of Yellow Warbler nests, which included replacement nests, monitored in each year of the study was: 119 in 1975, 148 in 1976, 64 in 1978, 59 in 1979, 44 in 1980, 126 in 1981, 157 in 1982, 237 in 1983, 260 nests in 1984, 225 in 1985, and 241 in 1986.

Yellow Warblers investigated in this study nested in a 7-km portion of the dune-ridge forest (~80 m wide; 56 ha), abutted by the lake on the north side and an extensive marsh of cattail (*Typha latifolia*) and reed (*Phragmites communis*) on the other (see map in Sealy 1980a). This portion of the ridge forest stretched from the west at Cram Creek eastward along the property of the Portage Country Club to the eastern edge of the property of the Delta Marsh Field Station (University of Manitoba). Yellow Warblers nested in the ridge for-

est predominantly in Sandbar Willow (*Salix interior*), Manitoba Maple (*Acer negundo*), Red-berried Elder (*Sambucus pubens*), Pin Cherry (*Prunus pensylvanica*), Choke Cherry (*P. virginiana*), and Red-osier Dogwood (*Cornus stolinifera*). Peach-leaved Willow (*S. amygdaloides*), Green Ash (*Fraxinux pennsylvanica*), and Eastern Cottonwood (*Populus deltoides*) also contributed to the overstory vegetation in this riparian habitat, but few Yellows Warblers nested in them (MacKenzie *et al.* 1982).

Methods

Adults of this sexually dichromatic, seasonally monogamous species (Reid and Sealy 1986) were mist-netted and colour-marked as after-hatch-year (AHY) males or females, following an annual banding protocol established late in 1974 and continued in each subsequent year of the study (e.g., Sealy 1980b; Sealy and Biermann 1983). Thus the first spring in which marked individuals were present in the study area was in 1975.

In addition, males and females were opportunistically captured and colour-banded near their nests (Cosens and Sealy 1986; Hobson and Sealy 1989). Colour-marking of nestlings and hatch-year (HY) individuals mist-netted prior to fall migration also began in 1975, and birds marked in that and subsequent years resulted in individuals of known age present in the study area in successive years. These individuals originally received a single coloured band, which, in combination with an aluminum band, denoted the year of hatch, so these birds became recognizable in their first spring as second-year (SY) individuals, and older in succeeding years. Upon recapture, year-marked individuals received two additional coloured bands that uniquely identified them. This marking program resulted in a sample of nests each year that were attended by at least one marked male or female (in several cases both adults were marked).

Yellow Warblers nested at densities up to 29 pairs/ha in the ridge forest in those years (Goossen and Sealy 1982; also see Sealy 1995). This density allowed dozens of nests to be discovered in most years before clutches were initiated, enabling day-to-day inspections as eggs were laid and inspections every one to four days through fledging of first and second broods. The extremely high nesting densities (Goossen and Sealy 1982), however, meant that only a small undetermined number of individuals could be marked, thus precluding the determination of the proportion of pairs that attempted second broods in each of the years in which double brooding was recorded.

I am confident that second broods were not attempted by any pairs in the 6 years in which none were recorded because I monitored a sample of nests, both those attended by marked birds and those attended by unmarked birds, equally diligently throughout all breeding seasons of the study (see Sealy 1995; Guigueno and Sealy 2010; Mazarolle *et al.* 2011).

Results

Double brooding was recorded in 20 pairs of Yellow Warblers of known age in 5 of the 11 years of the study (Table 1): 1975 (n = 1 pair), 1976 (n = 3 pairs), 1984 (n = 3 pairs), 1985 (n = 9 pairs), and 1986 (n = 4 pairs). At least one member of each pair was marked. Males (at 8 nests), females (at 5 nests), or both males and females (at 7 nests) were marked, thus permitting irrefutable confirmation of double brooding (Table 1).

These data suggest that all pairs remained together during the second nesting attempt, although polygyny, albeit infrequent in this population (Sealy 1984; Reid and Sealy 1986), could have resulted in a change of mate at nests where only one of the adults was marked. This would not change the fact, however, that double brooding occurred.

Among the 20 pairs with double broods were 4 whose second clutch was parasitized by a Brown-headed Cowbird (*Molothrus ater*) (3 in 1985 and 1 in 1986). None of the first nests of these or any of the other pairs that went on to attempt to raise a second brood were parasitized (Table 1). The frequency of parasitism by Brown-headed Cowbirds in this population of Yellow Warblers (also see Sealy 1995) was 26.1% of 119 nests monitored in 1975, 23.0% of 148 nests in 1976, 18.1% of 260 nests in 1984, 18.7% of 225 nests in 1985, and 17.8% of 241 nests in 1986.

Each pair's first nesting attempt successfully fledged at least one young, a necessary condition for double brooding. At one of the first nests in 1985, however, incubation was delayed about 3 days while the female replaced 3 of 4 eggs that had gone missing from the original nest (footnote 3 of Table 1). Clutches at 18 of the 20 first nests (90%) were initiated by 2 June (Table 1) in years where first eggs in the population were initiated on or up to 7 days before this date (also see table III *in* Sealy 1995).

All 7 marked pairs remained together for their second nesting attempt, lending support to the assumption that the members of the other pairs also did not change (although in these cases it was confirmed only that the same marked individuals (8 males and 6 females) remained for the second attempt). Eleven pairs, including the 4 pairs whose second clutches were parasitized, used their first nest for the second attempt. One female whose nest had been parasitized built a new nest over top of the one Brown-headed Cowbird and the two Yellow Warbler eggs that had been laid in the original nest. Nine females built a new nest for the second attempt (Table 1), in 5 cases because the original nests had disintegrated. The other 4 pairs built a new nest in another location nearby. None of the individuals with double broods was among the pairs that double brooded in previous or subsequent years, and no young produced in first or second nests, although banded, were subsequently captured in the study area.

Mean dates (nearest day and standard deviation) of initiation of the 20 first and second clutches were 30

TABLE 1. Dates and success of first and second clutches of marked Yellow Warblers (*Setophaga petechia*) with double broods at Delta Marsh, Manitoba, 1975–1986 (no data collected in 1977). CB = one Brown-headed Cowbird egg.

Year	Banded birds[2]	Date clutch initiated		Same nest used	No. of Yellow Warbler young fledged/eggs laid	
		First clutch	Second clutch		First clutch	Second clutch
1975[1]	After-hatch-year pair	2 June	1 July	No	1/5	0/4
1976	After-hatch-year pair	29 May	30 June	Yes	3/5	0/4
1976	After-hatch-year pair	2 June	6 July	Yes	3/4	0/2
1976	After-hatch-year pair	6 June	3 July	Yes	4/5	0/4
1984	After-second-year male and unmarked female	1 June	30 June	Yes	5/5	4/4
1984	After-second-year male and unmarked female	1 June	30 June	No	2/4	3/3
1984	After-second-year female and unmarked male	3 June	4 July	No	2/5	0/2
1985	After-second-year female and unmarked male	28 May	29 June	No	3/4	4/4
1985	Second-year male and unmarked female	27 May	28 June	Yes	5/5	3 + CB[3]/3+CB[3]
1985	After-second-year pair	27 May	30 June	No	5/5	4/4
1985	Second-hatch-year male and unmarked female	26 May	27 June	Yes	4/4	0/3
1985	After-second-year male and unmarked female	30 May	1 July	Yes	4/4	2 + CB/3+CB
1985	After-second-year female and unmarked male	30 May	27 June	No	3/4	4/4
1985	After-second-year male and unmarked female	28 May[3]	27 June	No	2/4	3/4
1985	After-second-year male and hatch-year female	29 May	29 June	Yes	4/5	4/4
1985	After-second-year male and unmarked female	27 May	1 July	Yes	5/5	3 + CB/3 + CB
1986	Second-year male and after-second-year female	28 May	28 June	No	?	3/4
1986	After-second-year male and unmarked female	28 May	22 June	Yes	2/4	2/2
1986	After-second-year female and unmarked male	30 May	5 July	Yes	5/5	0/0, CB buried[4]
1986	After-second-year female and unmarked male	28 May	25 June	No	2/4	3/4

[1]1 June 1975 = day 152 of the Julian calendar.

[2]At least one member of each pair was colour marked and, hence, could be aged when observed paired and attending a nest. Three age classes were recorded: second year (yearling), after hatch year (at least one year old), and after second year (at least two years old). All unmarked individuals were after hatch year.

[3]Female completed first clutch, of four eggs, on 31 May 1985, but on 2 June, only one egg of the original clutch plus one new egg were present; by 4 June, the final "clutch" of four eggs was present, from which two young fledged.

[4]Determined *post hoc*, but not included in the table is the female that buried one Brown-headed Cowbird egg plus two Yellow Warbler eggs under a new nest in the second nest.

May (SD 2.9 days) and 30 June (SD 3.2 days), respectively, and the mean number of days between initiation of first and second clutches was 30.2 days (SD 2.3 days). Mean initiation of first clutches by females with double broods followed the earliest dates that clutches were initiated in the population within 1 day (1975), 3–9 days (1976), 0–2 days (1984), 0–3 days (1985), and 1–3 days (1986). Initiation of second clutches preceded the last dates of the season for females still attempting to lay clutches by 6 days (1975), 0–7 days (1976), 3–7 days (1984), 7–11 days (1985), and 1–14 days (1986). The mean number of days between dates of fledging of the last nestling from first broods and dates of clutch initiation at unparasitized second nests (n = 16 nests) was 3.6 days (SD 1.5 days): 2 days (n = 2 nests), 3 days (7 nests), 4 days (4 nests), 5 days (1 nests), 6 days (1 nest), and 8 days (1 nest).

Parasitized nests were excluded from this analysis because of possible interference with initiation of the Yellow Warblers' clutches; indeed, a delay of 3 days in the completion of the clutch occurred at one nest parasitized in 1986 (Table 1), in which the Yellow Warbler buried the eggs. This nest eventually failed (see Clark and Robertson (1981) and Guigueno and Sealy (2010) for details of the chronology of laying by Yellow Warblers parasitized by Brown-headed Cowbirds).

Discussion

Documentation of double brooding

Data presented in Table 1 provide the first published evidence that Yellow Warblers attempt second broods in some years. Double brooding by Yellow Warblers has not been confirmed elsewhere in North America (but see below), but it has been confirmed in a non-migratory population on the Galápagos Islands, Ecuador (Snow 1966), located at the equator. Snow recorded a single marked pair that attempted to rear two broods in each of two consecutive years, but in both years the second attempt failed. He added (Snow 1966, page 46) that the "season is amply long enough for [rearing second broods], and two broods are probably common." The fact that double brooding has not been recorded at other sites, tropical or temperate, probably reflects the lack of observations of uniquely marked individuals throughout the breeding season.

These data support an earlier observation of an unmarked pair of Yellow Warblers that suggested double brooding in Manitoba, along the west shore of Lake Winnipeg, in 1978 (Bancroft 1979; also see Gollop 1979). Dates of initiation of the first and second clutches were in line with those presented for Delta Marsh and Lake Manitoba in Table 1. This pair's first nest was under construction on 26 May when it was first observed, and by 2 June it contained two Yellow Warbler eggs. An undetermined number of young had left the nest by 23 June, but by 7 July, the (same?) female was incubating 3 more eggs in the same nest from which the first brood had fledged. Again, an undetermined number of young, in the second brood, fledged by 27 July, as noted by feces on foliage near the empty nest and audible vocalizations of fledglings and adults in a nearby hedge (Bancroft 1979). Both adults fed young from the first brood, but it was not reported whether both cared for young in the second brood.

Post-hoc examination of the nest by H. W. R. Copland of the Manitoba Museum in Winnipeg after the second brood had fledged revealed the nest had been parasitized by a Brown-headed Cowbird during the laying of the second clutch, whereupon the Yellow Warbler buried the Brown-headed Cowbird egg plus two of her own eggs, one of which was broken, under a new nest, and started again. The time spent burying the Brown-headed Cowbird egg and her own eggs, reconstructing the nest, and replacing the initial eggs of the second clutch suggests the final clutch was initiated on 28 or 29 June, consistent with the dates of initiation of second clutches at Delta Marsh, including the nest parasitized in 1986 in which the Yellow Warbler buried the Brown-headed Cowbird and her first two eggs (Table 1).

Additional irrefutable records of double brooding by Yellow Warblers came to light during the review of this manuscript. One is in a population nesting at the northern limit of the species' range, near Inuvik, Northwest Territories (68°21'N, 133°45'W), and the other is near Revelstoke, British Columbia (50°57'N, 118°10'W) (Anna Drake, personal communication). Near Revelstoke, four cases of double brooding were recorded over eight years at a latitude similar to that of Delta Marsh. In 2004, a second-year female paired with an after-hatch-year male initiated first and second clutches on 25 May and 23 June, respectively. Three young fledged from each clutch. In 2005, two cases involved after-second-year females (one the female with the double brood in 2004 paired with the same male), which initiated first clutches on 27 and 30 May (fledging 5 and 3 young, respectively), and second clutches on 24 and 28 June, respectively (fledging 3 young from each nest). In 2011, an after-second-year female produced a maximum of three fledglings in the first clutch (initiated 30 May) and she produced a second clutch (date of initiation unknown). Dates of initiation of first and second clutches in this population were a few days earlier than those recorded at Delta Marsh (Table 1).

At Inuvik, Drake recorded a marked pair of after-hatch-year individuals that reared two broods in 2010, although the male was not observed while the female tended the second brood. First and second clutches were initiated on 1 June and 1 or 2 July, respectively, and the young fledged on 26 or 27 June and 23 or 24 July, respectively. These dates of initiation were remarkably similar to those recorded for first and second clutches at Delta Marsh (Table 1). Of the two cases at Delta Marsh in which first clutches also were initi-

ated on 1 June (both in 1984) (Table 1), the second clutches were initiated on 30 June, one or two days earlier than those at Inuvik.

Initiation of the earliest clutches by Yellow Warblers in other populations nesting at the northern limit of the range—Churchill, Manitoba (Briskie 1995), Yukon (Sinclair *et al.* 2003), and Alaska (Kessel 1989)—has not been recorded before the middle of June. Briskie (1995, page 539), commenting on the length of the breeding season of the Yellow Warbler at Churchill, observed some clutches that were replaced after failure early in the season, but found "… no evidence of double-brooding and [stated that] it is unlikely to occur. In the average year, even the earliest nests do not fledge young before late July and any second brood would require birds to remain in the area well past the end of the short subarctic summer." The dynamics of breeding of this and other species at the northern limit of their range require additional study, especially when temperatures are increasing.

Implications of double brooding

The proportion of pairs with double broods recorded in the population in suitable years at Delta Marsh is not known but its determination was likely influenced, in the first instance, by the availability of marked pairs and, more importantly, by the number of marked individuals whose first nests managed to survive through fledging, where ~60% of all nesting attempts by Yellow Warblers are depredated or fail due to inclement weather (Goossen and Sealy 1982; Guigueno and Sealy 2010). Probably no more than 5–10% of pairs attempted to rear second broods in the 5 years in which they were recorded, but double brooding also may have occurred in 4 additional years of the study (1978, 1980–82, see table III *in* Sealy 1995) that experienced similar nesting phenology. Nests tended by the marked pairs in those years may have failed before second clutches could be initiated, although if double brooding occurred, I should have recorded re-use of some first nests by unmarked pairs. Spring temperatures in 1979 and 1983 were lower and first clutches were not laid until 9 and 12 June, respectively (table III *in* Sealy 1995), probably too late for double brooding.

Within the limits of the small sample size of Yellow Warbler nests parasitized by Brown-headed Cowbirds (all of them second nests) (Table 1), it is noteworthy that parasitism was rejected at one of the four nests. Females tend to bury Brown-headed Cowbird eggs in the latter portion of the clutch-initiation season, but almost all females accept Brown-headed Cowbird eggs towards the end of the breeding season, when they are running out of time (Clark and Robertson 1981; Sealy 1995; Guigueno and Sealy 2010). This single instance of burial was unusual because it was initiated only two or three days before the last Yellow Warbler eggs of the season were laid at Delta Marsh in 1986 (table III *in* Sealy 1995).

Short-lived individuals (Klimkiewicz *et al.* 1983) might be expected to raise more than one brood in years when conditions are favourable (Evans Ogden and Stutchbury 1996), but they would have to be responsive to early spring temperatures. In a study of arrival and clutch initiation by Yellow Warblers over 30 years at Delta Marsh, Mazerolle *et al.* (2011) reported that individuals exhibited considerable plasticity in the dates of clutch initiation in response to mean May temperatures. This plasticity was observed only at the beginning of the breeding season, as Yellow Warblers molt and migrate early (Morton 1976) and arrive on the wintering grounds from Mexico south to Peru where they compete for feeding territories, as early as late August (Neudorf and Tarof 1998). Rigid scheduling of molt and migration may preclude attempts to rear second broods, except in early seasons, but this may become more frequent with increasing temperatures.

Acknowledgements

I thank J. Briskie, D. Busby, H. den Haan, J. Goossen, K. Hobson, D. MacKenzie, R. Olenick, G. (Biermann) Pohajdak, J. Porter, and G. Sutherland for assistance in the field during the early years of the research on songbirds at Delta Marsh, Manitoba, which included considerable assistance with banding and colour-marking. I thank an anonymous reviewer and Anna Drake for constructive comments offered during the review of the manuscript. In addition, I would like to thank Anna for allowing me to include the record of double brooding by a pair of Yellow Warblers at an even more northerly latitude and D. J. Green, M. Hepp, and S. P. Quinlan for providing data from a site near Revelstoke, British Columbia. This work was funded chiefly by the Natural Sciences and Engineering Research Council of Canada, augmented by substantial in-kind support provided by the Delta Marsh Field Station (University of Manitoba).

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Received 6 June 2013
Accepted 8 July 2013

Asynchronous Breeding and Variable Embryonic Development Period in the Threatened Northern Leopard Frog (*Lithobates pipiens*) in the Cypress Hills, Alberta, Canada: Conservation and Management Implications

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Randall, Lea A., Lynne D. Chalmers, Axel Moehrenschlager, and Anthony P. Russell. 2014. Asynchronous breeding and variable embryonic development period in the threatened Northern Leopard Frog (*Lithobates pipiens*) in the Cypress Hills, Alberta, Canada: conservation and management implications. Canadian Field-Naturalist 128(1): 50–56.

Understanding breeding phenology is critical for establishing monitoring strategies, comprehending population dynamics, and developing conservation actions for at-risk species, such as the Northern Leopard Frog *(Lithobates pipiens)*. The timing of spawning and hatching in the Northern Leopard Frog may be highly variable depending on regional environmental conditions, which can make establishing the timing of surveys difficult. In spring 2006, eggs were laid over 30 days (24 April to 23 May) and hatching occurred over 2 weeks (14–28 May) at three neighbouring ponds in Cypress Hills, Alberta, Canada. Although spawning occurred over a month, all eggs hatched within a 2-week period, indicating variable embryo development rate. Among 26 egg masses, eggs laid later in the season developed approximately four times faster than those laid earlier, and Akaike information criterion-ranked models suggested that both Julian date and water temperature were important predictors of embryo development rate: later spawning date and warmer water were associated with faster rates. Some egg masses survived colder temperatures than previously reported for this species. Asynchronous breeding and variable development rates reveal the need to conduct multiple surveys over the breeding season, even within a small geographic area, to document reliably the presence of egg masses and identify breeding habitat. Identification of key breeding habitat is necessary to mitigate human-caused disturbances of such regionally imperiled species.

Key Words: Northern Leopard Frog; *Lithobates pipiens*; amphibian; breeding; egg; conservation; embryo development; spawning period; phenology; Cypress Hills; Alberta

Introduction

Breeding phenology and the time between spawning and hatching may be highly variable within and among populations of amphibians (Thumm and Mahony 2002; Ryan and Plague 2004) as a result of an assortment of exogenous and endogenous factors (Reading 1998; Oseen and Wassersug 2002; Grant *et al.* 2009). This variability can make timing of population surveys challenging.

Industrial development continues to increase in Alberta, particularly in association with oil and gas extraction, and may negatively affect wildlife unless proper mitigation measures can be implemented. Permits for industrial exploration and extraction often stipulate a requirement for amphibian surveys before land development if at-risk amphibians are predicted to inhabit the area (Dr. David Prescott, Species at Risk Biologist, Alberta Environment and Sustainable Resource Development, personal communication, 29 March 2012). However, for these surveys to be effective, they must be carried out at a time and in a manner appropriate for the species of interest.

Once widely distributed and abundant in North America, the Northern Leopard Frog (*Lithobates pipiens*) disappeared from much of the western portion of its range in the 1970s and 80s (Roberts 1981*; Leonard *et al.* 1999), perhaps due to such factors as disease, drought, competition by invasive species, and habitat loss and fragmentation (COSEWIC 2009*). As a result, the western boreal–prairie populations of Northern Leopard Frogs are designated of "special concern" by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC 2009*) and "threatened" under Alberta's Wildlife Act (AESRD 2012*).

We investigated predictors of spawning time and embryo development rate of Northern Leopard Frogs, such as temperature and time of year, as part of a larger study of tadpole microhabitat selection and juvenile dispersal behaviour. Natural history observations of this type may be useful for improving the probability of detection by providing information regarding the timing of the breeding period and the frequency of surveys required to identify and protect important habitat.

Study Area

Our study was conducted in and near Cypress Hills Interprovincial Park (49°39'N, 110°01'W) which straddles the border between Alberta and Saskatchewan and is just north of the Sweetgrass Hills of Montana (Figure 1). The Alberta portion of the Cypress Hills is char-

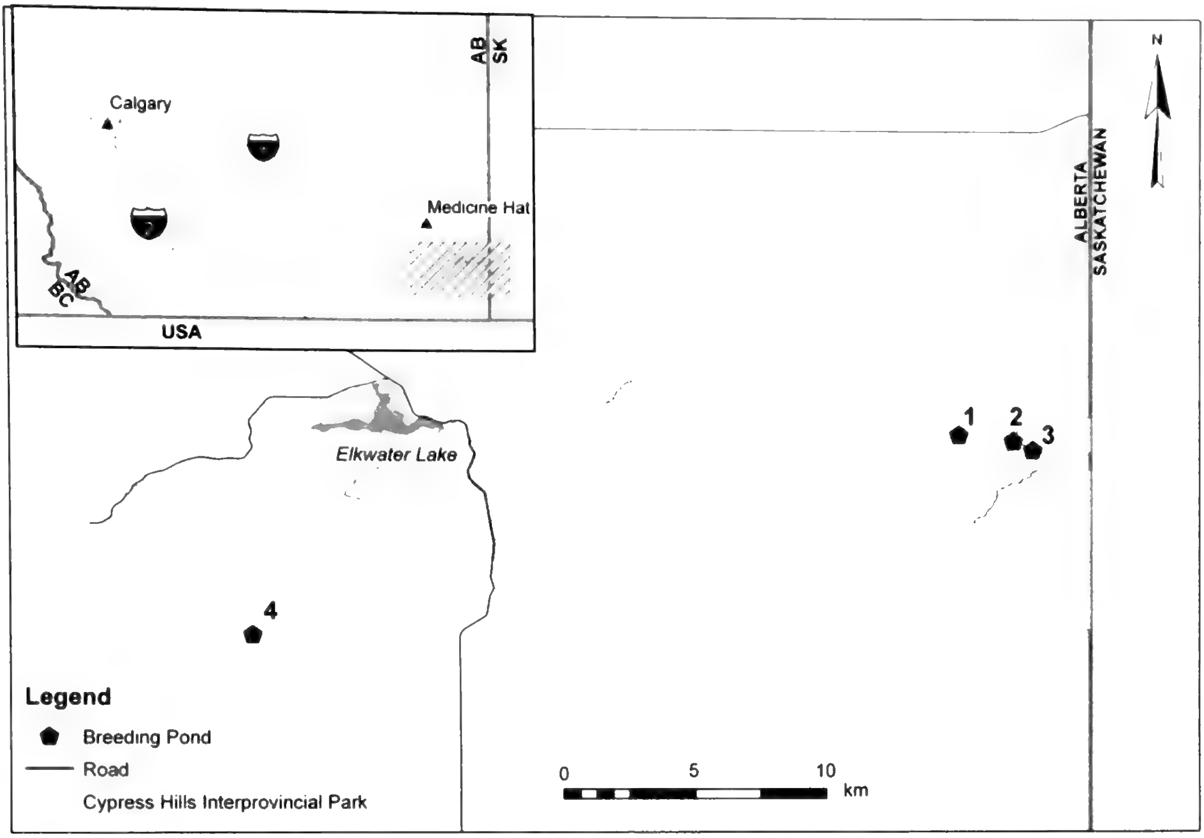

FIGURE 1. Locations of four Northern Leopard Frog (*Lithobates pipiens*) breeding ponds surveyed in 2006 in and near Cypress Hills Interprovincial Park, Alberta, Canada (49°39'N, 110°01'W).

acterized by grasslands and boreal forest. Elevation ranges from 1370 m to 1465 m, and average annual temperature is lower than that of the surrounding grassland plains (Greenlee 1981*). These environmental conditions likely present challenges to the reproductive success of Northern Leopard Frogs.

In 2006, we drove along roads and flew over the study area in a fixed-wing aircraft to identify potential Northern Leopard Frog breeding ponds within a 25-km radius of our main study pond (Pond 1, Figure 1). Although other breeding ponds may have been present, these four represented all known breeding ponds at the time.

Pond 1 was 0.1 ha in surface area and was surrounded by *Populus spp.* woodlands on the east, west, and south sides; the north side had a relatively steeper slope of mixed grass prairie (Fraser 2007). Ponds 2 and 3 had surface areas of 0.17 ha and 0.04 ha, respectively, and were also surrounded by mixed grass prairie and aspen woodland. Pond 4 had a surface area of 0.24 ha and was surrounded by mixed forest, mainly white spruce (*Picea glauca*) on the west and north sides and deadfall on the south and east sides.

Methods

Study organism

Adult Northern Leopard Frogs are medium-sized frogs, 5–10 cm long from snout to vent (Hine *et al.* 1981*; Russell and Bauer 2000). Within a population, breeding period ranges from a few days to a few weeks (Wells 1977). In Alberta, spawning occurs over a short interval between late April and early June (Russell and Bauer 2000; Kendell 2002) at temperatures of 10–25°C, although spawning may be prolonged if the temperature drops below this range (Hine *et al.* 1981*; Gilbert *et al.* 1994; Kendell 2002*). Females deposit 600–7000 eggs in a single egg mass, which they attach to submerged vegetation. Preferred water bodies are ephemeral or fishless permanent ponds or slow-moving backwaters of streams and rivers in shallow water (AESRD 2012*). The period from spawning to hatching may last from 5 days to 3 weeks (Russell and Bauer 2000; Werner *et al.* 2004) and metamorphosis typically occurs between July and August in Alberta (Kendell 2002*).

Observation techniques

Beginning approximately 30 minutes after sunset, we listened for breeding calls of adult male Northern Leopard Frogs for up to 20 minutes (AESRD 2013*). If calls were detected, we returned the following day to confirm spawning.

We conducted call and shoreline surveys from 25 April to 8 June 2006 and searched the shoreline of each pond at least once every 2 days for new egg masses to determine the duration of the breeding season and the embryo development period (Merrell 1977*; Dorcas *et*

al. 2010; Paton and Harris 2010). Individual egg masses were identified by differences in either their size or shape or the stage of development of the embryos (Merrell 1977*). Their location along the shoreline was marked with a flag to prevent counting an egg mass twice (Gilbert *et al.* 1994; Dougherty *et al.* 2005). During each survey, egg masses were identified as hatched or unhatched (egg mass intact). Hatching was confirmed when newly hatched tadpoles were seen aggregating around the egg mass, feeding on the remaining jelly.

For each egg mass, we measured its depth below the water surface, distance to adjacent masses, and distance from the shoreline using a metre stick. During shoreline surveys, we measured the temperature of the water within 10 cm of each egg mass using a Hanna pH pen thermometer. We considered the breeding season complete once male calling had ceased and no new egg masses had been observed for at least 2 weeks.

Statistical analysis

We ran a one-way ANOVA to determine whether ponds differed with respect to water temperature when egg masses were laid, followed by Tukey's honest significant difference (HSD) test. We assessed whether residuals were normally distributed using a Shapiro–Wilk goodness-of-fit test ($W > 0.93$). We used Julian date (JD) in our models to account for seasonal variation of environmental factors, such as photoperiod.

To evaluate predictive factors related to embryo development, we first performed an exploratory regression analysis of embryo development rate versus JD and water temperature (WT). To further investigate the relation of JD and WT to embryo development rate we used restricted maximum likelihood mixed-model regression (JMP, version 7, SAS Institute Inc., Cary, North Carolina, USA). Pond was a random factor; all other factors were fixed. We formulated a set of candidate models that all included pond alone, pond with JD or WT, or pond with both JD and WT in an additive model and with the interaction of JD and WT. Because collinearity of predictor variables can yield unstable parameter estimates and inflated standard errors (Quinn and Keough 2002), we verified that JD and WT were not highly correlated ($r^2 < 0.6$) before we included them together in a model (Royston and Sauerbrei 2008). We compared models using small-sample-size Akaike information criterion (AIC_c) to select the "best" model given a candidate set of models and considered models to have equivalent support if ΔAIC_c was < 2 (Burnham and Anderson 2004). We assessed the goodness-of-fit of the global model using a Shapiro–Wilk test ($W > 0.90$).

Results

Spawning occurred over 30 days at ponds 1–3, beginning on 24 April and ending 23 May (Figure 2).

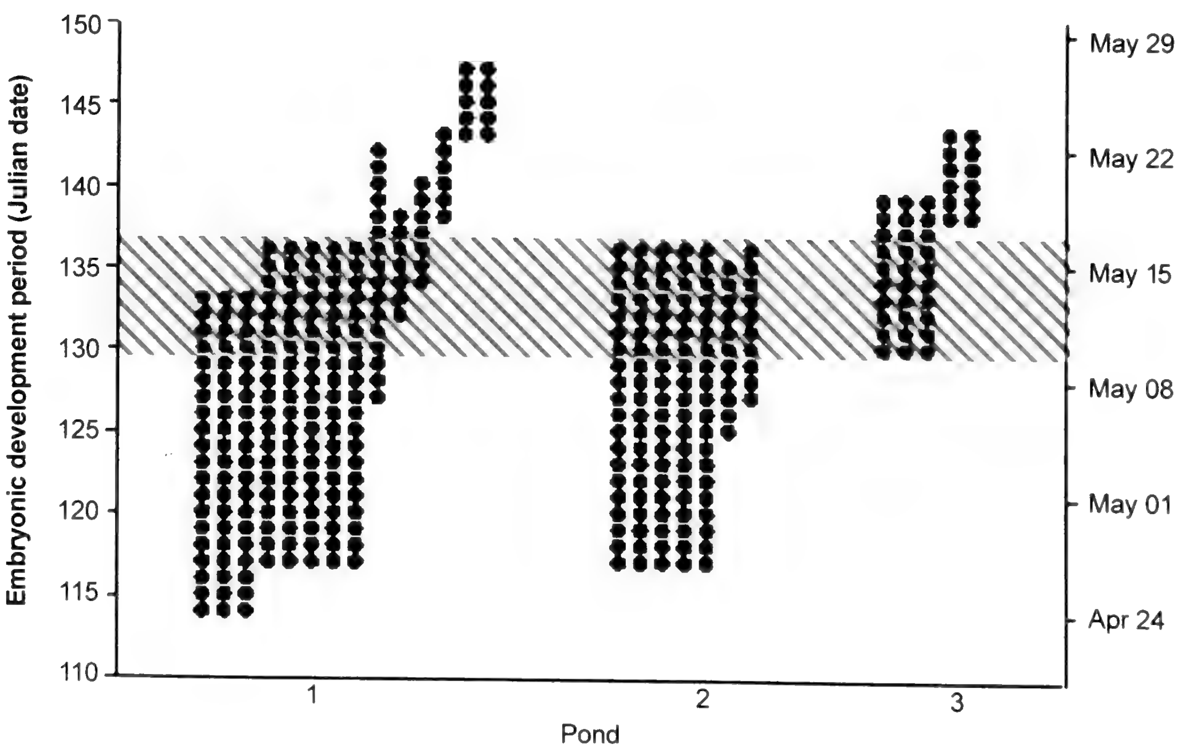

FIGURE 2. Development period for Northern Leopard Frog (*Lithobates pipiens*) eggs at ponds 1, 2, and 3 in Cypress Hills Interprovincial Park, Alberta (see Figure 1) in April and May 2006. Each column of black circles represents days from spawning to hatching for one of the 26 egg masses observed. The shaded area represents the period during which egg masses were present at all three ponds (10–17 May).

Although calling and spawning were confirmed at pond 4, we were unable to monitor egg masses because pollen blanketed more than half of the water surface, affecting our ability to observe them. Hatching occurred at the three remaining ponds over 2 weeks, beginning 14 May with the last eggs hatching on 28 May. We observed a total of 26 egg masses: 14 in pond 1, 7 in pond 2, and 5 in pond 3. Egg masses were laid within 2–10 cm of the water surface, typically grouped together in shallow areas within 2–3 m of the shoreline. All monitored egg masses survived to hatching, but we were unable to monitor the proportion of eggs that hatched successfully.

The onset of spawning differed by only 3 days between ponds 1 and 2, but occurred approximately 2 weeks later at pond 3. The WT near each egg mass on the day of spawning was significantly higher at pond 3 (17.4°C ± 1.9 [mean ± standard error], $r^2 = 0.40$, $F_{2,25} = 7.62$, $P = 0.0029$) than at ponds 1 and 2, but did not differ between ponds 1 and 2 (9.1°C ± 1.6 and 9.1°C ± 1.1, respectively). At ponds 1 and 2, egg laying first occurred on 24 and 27 April, respectively. Up to five egg masses were laid on the same day in ponds 1 and 2, and the spawning period lasted for almost a month. Egg masses were detected simultaneously at all three ponds during only 1 week, 10–17 May.

At the time eggs were laid WT ranged from 5.7°C to 25.8°C. At pond 1, WT dipped as low as 3°C during egg development (27 April). Time from spawning to hatching ranged from 5 to 20 days and decreased with JD at laying (Figure 3). Eggs deposited at the beginning of the breeding season (24 April) took about four times as long to hatch as the last eggs laid (23 May).

Although we found a strong, negative relation between embryonic development period and JD, the relation between that period and spawning temperature was not as strong (Figure 4). The top model, with 93% of the AIC_c weight, was an additive model that included WT and JD (Table 1). No other models were < 2 ΔAIC_c of the top model.

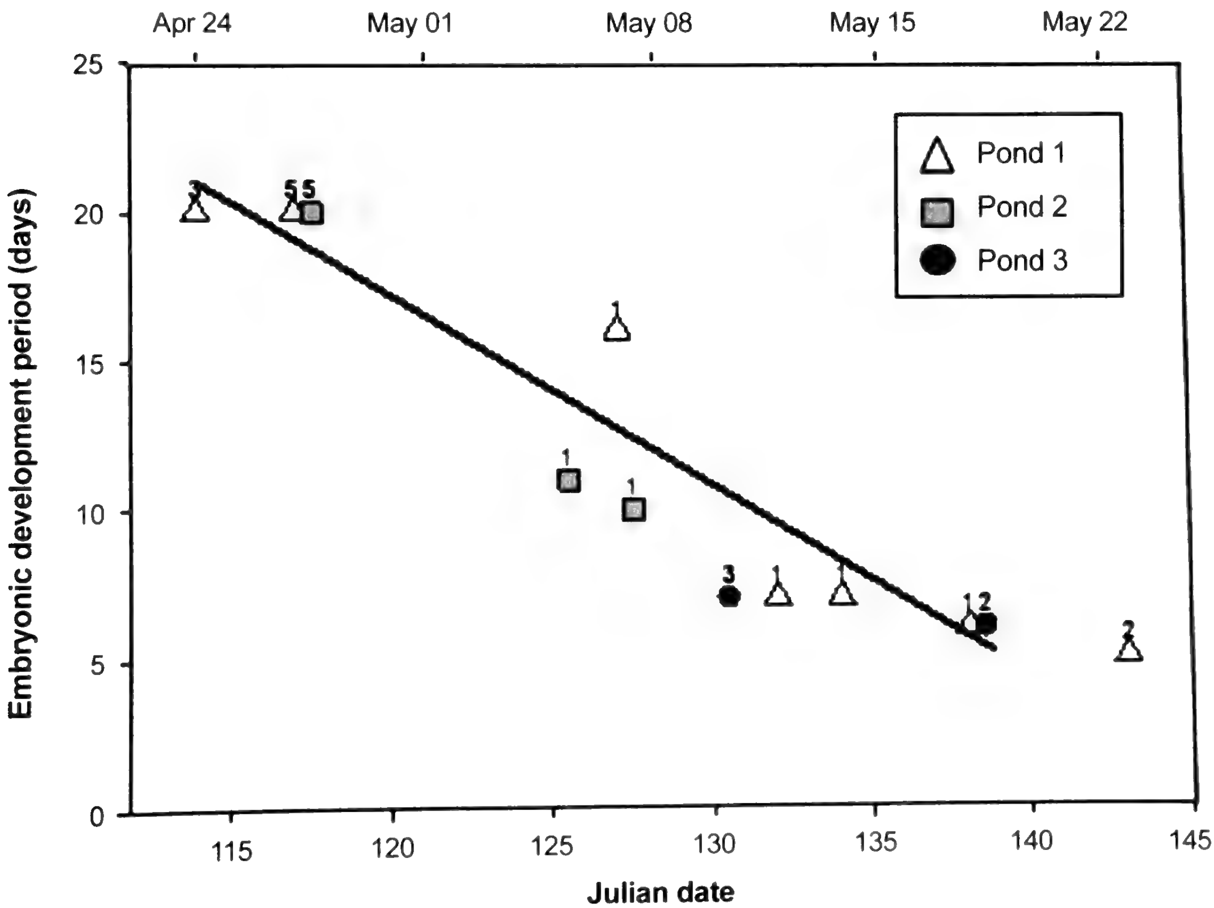

FIGURE 3. Relation between development period and Julian date (24 April–28 May 2006) for 26 Northern Leopard Frog (*Lithobates pipiens*) egg masses at ponds 1, 2, and 3 in Cypress Hills Interprovincial Park, Alberta (see Figure 1). The numbers above each symbol represent the number of egg masses laid on that date. Symbols for ponds at which egg masses were laid on the same date have been slightly offset ($r^2 = 0.91$).

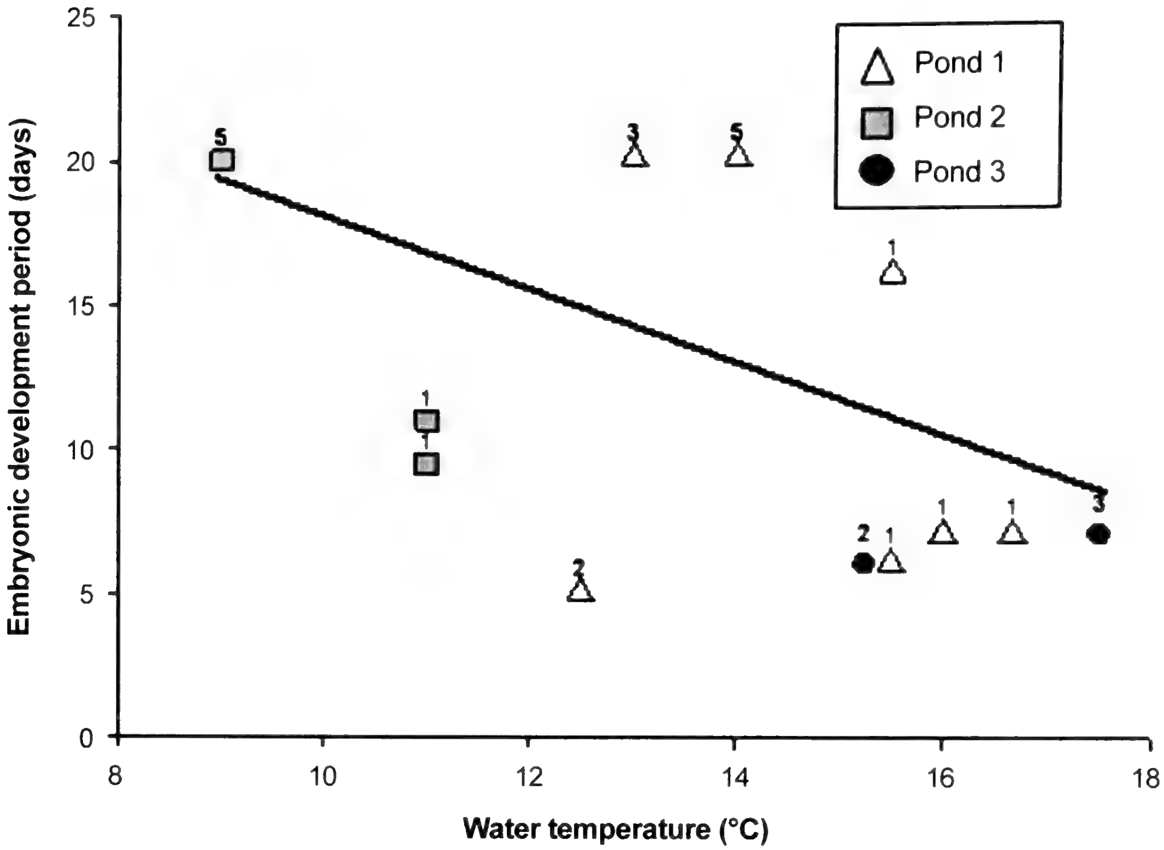

FIGURE 4. Relation between development period (24 April–28 May 2006) and spawning temperature for 26 Northern Leopard Frog (*Lithobates pipiens*) egg masses at ponds 1, 2, and 3 in Cypress Hills Interprovincial Park, Alberta (see Figure 1). Numbers above each symbol represent the number of egg masses laid at that water temperature. Symbols for ponds at which egg masses were laid at the same water temperature have been slightly offset ($r^2 = 0.32$).

TABLE 1. Variation in development period of Northern Leopard Frog (*Lithobates pipiens*) eggs with Julian date (JD) and water temperature (WT). The top model was selected using Akaike information criterion adjusted for small sample size (AIC_c).

Model	–2LL	*K*	AIC_c	ΔAIC_c	AIC_c weight
Embryo development period = Pond + JD + WT	102.59	5	115.59	0.00	0.93
Embryo development period = Pond + JD	111.24	4	121.14	5.55	0.06
Embryo development period = Pond + JD +WT + JD*WT	107.59	6	124.01	8.42	0.01
Embryo development period = Pond + WT	158.07	4	167.97	52.38	0.00
Embryo development period = Pond	164.85	3	171.95	56.36	0.00

Note: –2LL is –2*model log-likelihood, *K* is the number of parameters in the model. ΔAIC_c is the difference between the AIC_c of each model and the top model.

Discussion

The onset of spawning was not synchronous in our study area and varied by over 3 weeks among our ponds. However, spawning was often synchronous within a pond, with several egg masses laid on a single day. The spawning period was also protracted, lasting up to 30 days at a single breeding pond (pond 1). The duration of the breeding season and the embryonic development period was consistent with other published reports (Merrell 1968; Wells 1977; Russell and Bauer 2000; Werner *et al.* 2004). It is interesting to note that, whereas spawning occurred over the course of a month, all eggs hatched within a 2-week period with the first eggs deposited taking almost four times as long to develop as the last eggs laid.

Eggs were laid at WT ranging from 5.7°C to 25.8°C, which is consistent with known egg temperature tolerances for this species (Moore 1939, 1949). However, our minimum spawning temperature was more than 2°C colder than that recorded for Northern Leopard

Frogs in Quebec, which do not spawn at WT below 8°C (Gilbert *et al.* 1994). In addition, WT at one of our ponds dropped to 3°C during the development period, which is 2°C below the reported threshold for normal embryonic development in this species (Moore 1949). However, the temperature at the centre of an egg mass can be up to 2°C warmer than the surrounding water (Hassinger 1970). Although the four affected egg masses survived to hatching, we were unable to evaluate whether the embryos had developed normally.

The top model for embryonic development period included both JD and WT as predictive variables, suggesting that temperature alone is not sufficient to explain differences in development period, which might also be affected by seasonal differences in the region. However, there was no evidence that the effect of temperature on development changed over time (the interactive model was > 8 ΔAIC_c from the top model). Although it has long been known that the development of Northern Leopard Frogs is temperature dependant (Atlas 1935; Moore 1939), clearly this is not the only factor affecting embryo development period.

Conservation and Management Implications

Industrial development permits issued by regulators often stipulate that developers determine whether at-risk species, such as the Northern Leopard Frog, are present and establish appropriate mitigation strategies to reduce or eliminate negative impacts of their activities. Often only single surveys are conducted to determine the presence or absence of at-risk amphibians (Kendell 2003*). Our results suggest that inappropriately timed breeding surveys may fail to detect Northern Leopard Frogs and could, thus, limit the ability to develop appropriate strategies to conserve this species.

Even within our small study area, egg masses would have been observed in all three ponds during only 1 week — a narrow timeframe for the completion of effective and comprehensive egg-mass surveys. Because breeding phenology is likely to vary annually, regionally, and locally, we recommend that researchers adjust the timing of their surveys so that they are relevant to each specific site. To identify breeding ponds, multiple breeding surveys separated in time should be conducted. The need to adjust the timing and number of surveys necessary to identify breeding sites is not unique to Northern Leopard Frogs (AESRD 2013*). As such, we recommend that breeding phenology be considered when developing monitoring strategies or industrial mitigation procedures for amphibians elsewhere.

Acknowledgements

All research was conducted in compliance with University of Calgary Animal Care Protocol BI 2005–39 and the Calgary Zoo BRRC 2005–05 approval number. We are grateful for funding provided by Husky Energy and Cenovus Energy Ltd. We thank Typhenn Brichieri-Colombi for providing the map of the study area.

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Received 16 September 2013
Accepted 18 November 2013

Diet of the Pacific Sand Lance (*Ammodytes hexapterus*) in the Salish Sea, British Columbia, in the 1960s

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Hipfner, J. Mark, and Moira Galbraith. 2014. Diet of the Pacific Sand Lance (*Ammodytes hexapterus*) in the Salish Sea, British Columbia, in the 1960s. Canadian Field-Naturalist 128(1): 57–62.

The diet of the Pacific Sand Lance (*Ammodytes hexapterus*) was quantified from the stomach contents of 115 Pacific Sand Lance caught in the Strait of Georgia and Saanich Inlet (Vancouver Island) in the Salish Sea, British Columbia, in the spring and summer of 1966, in the Strait of Georgia in the spring and summer of 1967, and in the Strait of Georgia and Saanich Inlet in the spring and summer of 1968. There were 12 major taxa of prey in diets, 8 of which were Crustacea. Based on an index of relative importance, copepods were the dominant prey in 1966 and 1968, but not in 1967, when cladocerans, larvaceans, and teleosts also were common. The copepods *Pseudocalanus* spp. and *Calanus marshallae* were the only taxa to appear in diets in all three years. *Pseudocalanus* dominated the copepod component of diets in 1966, when sampling occurred in July; unspecified copepod nauplii (an early larval stage) were dominant in 1967 and 1968, when sampling occurred earlier (April to June). With the profound changes that have occurred in the Salish Sea over recent decades, these data can serve as a baseline for comparison.

Key Words: Pacific Sand Lance; *Ammodytes hexapterus*; diet; interannual variation; decadal variation; Strait of Georgia; Salish Sea; British Columbia

Introduction

In marine systems of the temperate northern hemisphere, the six species of sand lances (*Ammodytes* spp.) often act as important trophic links between zooplankton and the broad suite of predators that feed on small forage fishes (Wanless *et al.* 2005). The energy densities, growth rates, and fecundity of sand lances all vary spatially and temporally (Robards *et al.* 2002; Wanless *et al.* 2005), and this suggests that feeding conditions for sand lances can be highly variable.

The Pacific Sand Lance (*Ammodytes hexapterus*) is a vital component of northeastern Pacific Ocean food webs (Beacham 1986; Borstad *et al.* 2011). Despite its ecological importance, however, information on the diet of this species is extremely limited. A recent study quantified the diet of the Pacific Sand Lance at several sites along British Columbia's outer coast in the summers of 2009, 2010, and 2011 (Hipfner and Galbraith 2013).

Here, we have collated and analyzed data collected in the protected inner waters of the Salish Sea in the spring and summer of 1966, 1967, and 1968 (Barraclough and Fulton 1968a*, 1968b*; Barraclough *et al.* 1968*; Robinson *et al.* 1968*; Robinson 1969*). Because the Salish Sea ecosystem has undergone dramatic changes since that time (Therriault *et al.* 2009), these data can serve as a baseline for comparison.

Methods

Pacific Sand Lance were collected in surface trawls in waters of the Salish Sea off the coast of British Columbia: 8 were collected between 4 and 8 July 1966 in the Strait of Georgia and Saanich Inlet (southern Vancouver Island), 26 were collected between 5 and 9 June 1967 in the Strait of Georgia, and 81 were collected between 23 April and 7 June 1968 in the Strait of Georgia and Saanich Inlet. The gastrointestinal tracts of the 115 Pacific Sand Lance were excised with scalpel and forceps and were placed in vials filled with 15% buffered formalin.

In the laboratory, the excised tracts were washed over a 0.063 mm mesh to remove the formalin, which was captured for neutralization treatment and disposal. Each stomach was then separated out, transferred to a 1 mm gridded Petrie dish, and slit longitudinally under a Wild M4 dissecting microscope with ocular micrometer. The contents were removed using water from a squeeze bottle and then the items were counted. Their life stage was determined and they were identified to the lowest taxonomic level possible. Some stomach contents were fresh and in a condition that allowed the prey to be identified to species, but most contents had been at least partially digested. As a result, the representation of soft-bodied prey types such as larvaceans in diets could have been underestimated (Barraclough and Fulton 1968a*, 1968b*; Barraclough *et al.* 1968*; Robinson *et al.* 1968*; Robinson 1969*).

For this report, dry weight estimates were assigned to each species and stage based on weight vs. length regressions from Fulton (1968) and McCauley (1984), as well as direct lab measurements. Total length was used for most prey items, the exceptions being fork length in the case of larval fish and prosome length in the case of copepods.

To facilitate direct comparison with information collected elsewhere in British Columbia, we analyzed the data as described in Hipfner and Galbraith (2013). An

index of relative importance (Pinkas *et al.* 1971) was calculated to quantify the importance of each prey type in Pacific Sand Lance diets in each year. The formula is:

(1) I_{RI} = the proportion of all non-empty stomachs that contained prey type (i) × (the proportion by number of prey type (i) item relative to all prey types + the proportion by dry mass of prey type (i) relative to all prey types).

Following Santic *et al.* (2012), we then standardized this index for each prey type to a scale of 0–100 using the formula:

(2) $\%I_{RI} = 100 \times [I_{RI} \times (\sum I_{RI}^{-1})]$.

When a predator consumes exclusively small prey, there tend to be strong correlations among the three component measures of I_{RI} (percentage frequency of occurrence, percentage by number of individual prey items, and percentage mass of prey), and these correlations can exaggerate differences in the importance of prey types (Macdonald and Green 1983). Therefore, we also report each of the three component measures for all prey types that constituted 10% or more of the $\%I_{RI}$ in at least one of the three years.

Results

The fork lengths of the collected Pacific Sand Lance varied from 10 to 115 mm, with the mean fork length being longer the later in the season that sampling occurred (Figure 1). Based on Figure 5 in Blackburn and Anderson (1997*) and Figure 7 in Robards *et al.* (2002), we assume that all Pacific Sand Lance sampled in 1966 and 1968 were young-of-year fish (age 0), as were the vast majority in 1967 (those <100 mm in fork length). Food was found in the stomachs of all but 1 of the 115 Pacific Sand Lance, the lone exception occurring in 1967.

Across the three years, there were 12 major taxa of prey in Pacific Sand Lance stomachs, including 8 groups of crustaceans, as well as trematodes, molluscs, larvaceans (plankton), and teleosts (fish). However, prey from only 2 (in 1968), 4 (1966), and 10 (1967) of the 12 major taxa were present in any one year (Table 1). Of the 12 major taxa, copepods were by far the dominant group in 1966 ($\%I_{RI}$ = 97.0) and 1968 (99.9), but not in 1967 (21.5), when cladocerans (33.1), larvaceans (18.0), and teleosts (25.7) also were common (Figure 2) (Table 2).

The copepods *Pseudocalanus* spp. and *Calanus pacificus* were the only prey types recorded in all three years (Table 1). In considering just the copepod component of the diet of the Pacific Sand Lance, *Pseudocalanus* dominated in 1966 ($\%I_{RI}$ = 72.8), whereas unspecified copepod nauplii dominated in both 1967 ($\%I_{RI}$ = 72.0) and 1968 ($\%I_{RI}$ = 64.1) (Table 3) (Figure 3). Three large calanoids—*Calanus pacificus*,

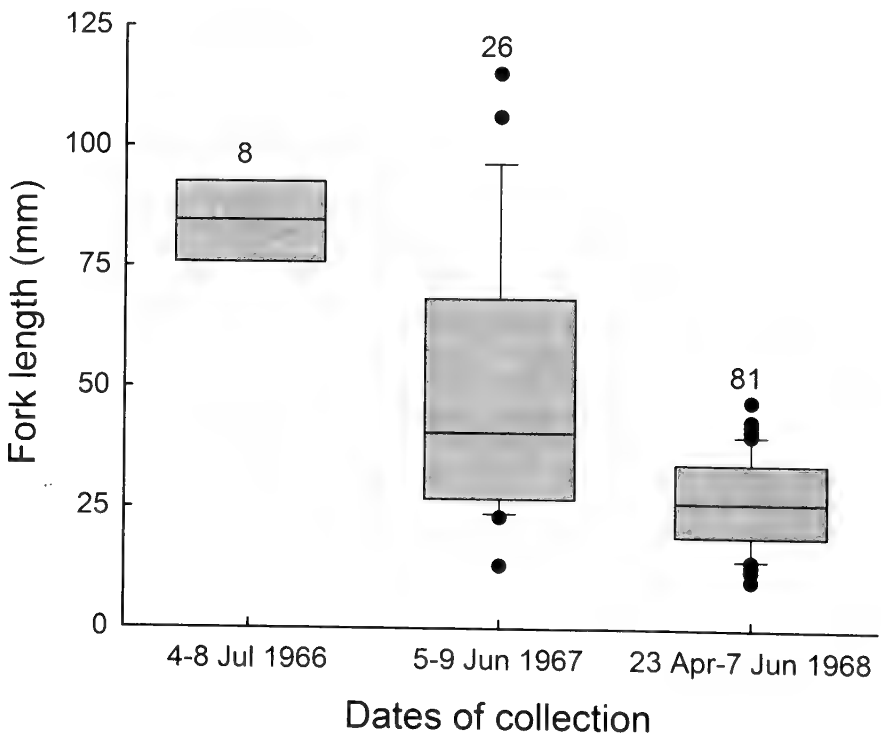

FIGURE 1. Fork lengths of Pacific Sand Lance (*Ammodytes hexapterus*) collected in trawl surveys in the Salish Sea, British Columbia, in relation to the date of sampling. Box plots show means, 25th and 75th percentiles, 5th and 95th percentiles (whiskers), and outliers. Sampling occurred from 4 to 8 July 1966 in the Strait of Georgia and Saanich Inlet, from 5 to 9 June 1967 in the Strait of Georgia, and from 23 April to 7 June 1968 in the Strait of Georgia and Saanich Inlet.

TABLE 1. Prey taxa and life stages recorded in the stomach contents of Pacific Sand Lance (*Ammodytes hexapterus*) in the Salish Sea, British Columbia, in 1966–1968.

Major taxa	Sub-type/species	1966 (n = 8)	1967 (n = 26)	1968 (n = 81)
Trematodes	—	0	Yes	0
Molluscs	Pelecypoda	0	Yes	0
Crustaceans				
Cirripeds	Barnacle	0	Yes (nauplii)	0
	Balanus	0	Yes (eggs)	0
Cladocerans	*Podon*	Yes	Yes	0
Ostracods	*Alacia minor*	0	Yes	0
Copepods	Copepod	0	Yes (eggs, nauplii, copepodites)	Yes (eggs, nauplii, copepodites)
	Acartia longiremis	Yes	0	0
	Calanus pacificus	Yes	Yes	Yes
	Microcalanus	0	0	Yes
	Pseudocalanus	Yes	Yes	Yes
	Cyclopoid	0	Yes	0
	Neocalanus plumchrus	0	Yes	0
	Scolecithricella minor	Yes	0	0
	Paraeuchaeta elongata	0	0	Yes
Hyperiids	*Themisto pacifica*	0	Yes	0
Mysids	—	Yes	0	0
Euphausiids	Euphausiid	0	0	Yes (eggs)
Decapods	Brachyuran	Yes (zoea)	Yes (megalops)	0
Larvaceans	*Oikopleura*	0	Yes	0
Teleostei	—	0	Yes	0

Neocalanus plumchrus, and *Paraeuchaeta elongata*—were the dominant copepods in terms of mass in 1966, 1967, and 1968, respectively, despite being present in small numbers and in few stomachs—especially *P. elongata* (Figure 3). Although *Paraeuchaeta elongata* constituted 44.97% of the copepod component of diets in terms of mass in 1968, it was present in very small numbers (2.50%) in very few stomachs (2.75%) and thus had $\%I_{RI}$ of <2%. *Scolecithricella minor* (in 1966) and unspecified copepodites (in 1968) were the only other prey that constituted ≥10% of copepod $\%I_{RI}$ in at least one of the three years (Table 3) (Figure 3).

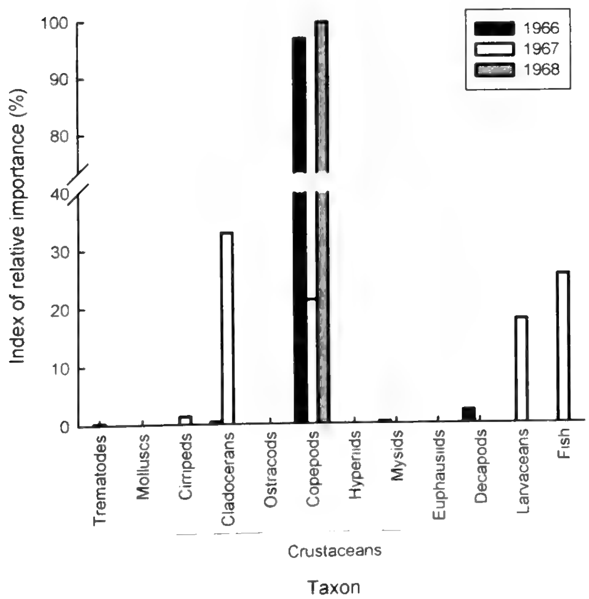

FIGURE 2. Indices of relative importance ($\%I_{RI}$) of the 12 major taxa of prey consumed by Pacific Sand Lance (*Ammodytes hexapterus*) in the Salish Sea, British Columbia, in each of three years (1966, 1967, and 1968).

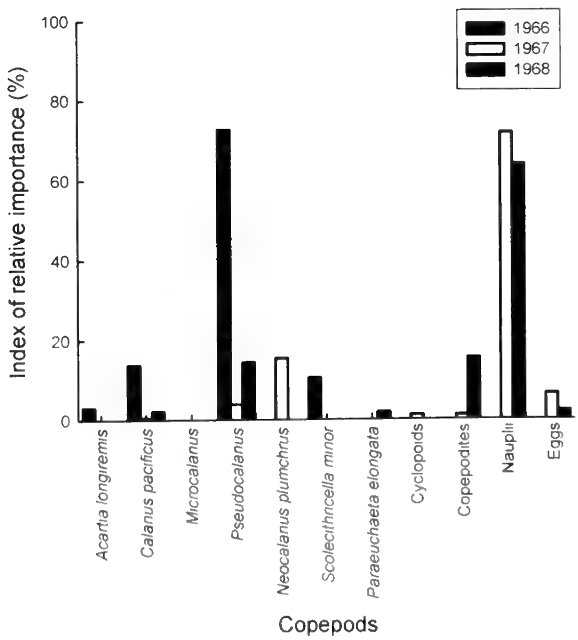

FIGURE 3. Indices of relative importance ($\%I_{RI}$) of the 11 taxa and life stages of unspecified copepod prey consumed by Pacific Sand Lance (*Ammodytes hexapterus*) in the Salish Sea, British Columbia, in each of three years (1966, 1967, and 1968).

TABLE 2. Values (percentage frequency, percentage by number of individual prey items, and percentage mass) used to calculate the index of relative importance (I_{RI}) for major prey groups with $\%I_{RI}$ ≥10% of the diets of Pacific Sand Lance (*Ammodytes hexapterus*) in the Salish Sea, British Columbia, in at least one of the three years from 1966 to 1968.

	1966			1967			1968		
Prey group	Percentage frequency	Percentage of prey items	Percentage mass	Percentage frequency	Percentage of prey items	Percentage mass	Percentage frequency	Percentage of prey items	Percentage mass
Cladocerans	12.50	3.03	2.34	34.62	45.67	1.18	0	0	0
Copepods	100	89.39	71.43	76.92	9.60	4.10	100	97.32	99.13
Larvaceans	0	0	0	11.54	36.66	39.81	0	0	0
Fish	0	0	0	23.08	1.53	53.14	0	0	0

TABLE 3. Values (percentage frequency, percentage by number of individual prey items, and percentage mass) used to calculate the index of relative importance (I_{RI}) of copepod prey taxa with $\%I_{RI}$ ≥10% of the diets of Pacific Sand Lance (*Ammodytes hexapterus*) in the Salish Sea, British Columbia, in at least one of the three years from 1966 to 1968. Note that *Paraeuchaeta elongata* constituted 44.97% of the copepod component of diets in terms of mass in 1968, but was present in very small numbers (2.50%) in very few stomachs (2.75%) and thus had $\%I_{RI}$ of <2%; it was therefore excluded from this table.

	1966			1967			1968		
Prey group	Percentage frequency	Percentage of prey items	Percentage mass	Percentage frequency	Percentage of prey items	Percentage mass	Percentage frequency	Percentage of prey items	Percentage mass
Pseudocalanus	75.00	55.93	22.62	15.38	5.32	1.34	33.75	11.16	16.64
Calanus pacificus	12.50	16.95	72.13	3.85	0.76	2.03	6.25	1.30	20.37
Neocalanus plumchrus	0	0	0	3.84	14.07	93.74	0	0	0
Scolecithricella minor	37.50	18.64	3.93	0	0	0	0	0	0
Copepodites	0	0	0	11.54	1.90	0.46	43.75	16.96	6.02
Copepod nauplii	0	0	0	30.77	60.84	2.21	65.00	53.04	11.30

Discussion

The Pacific Sand Lance is a vital component of northeastern Pacific Ocean food webs (Beacham 1986; Gjerdrum *et al.* 2003), so there is need for a thorough understanding of its trophic relations. In the protected inner waters of the Salish Sea, 12 major prey taxa were found in its diet: 8 crustacean groups, plus trematodes, molluscs, larvaceans, and teleosts. This suite of prey taxa is similar to that reported for other species of sand lances (Scott 1973; Sekiguchi 1977; Richards 1982) and for the Pacific Sand Lance elsewhere (Blackburn and Anderson 1997*), including at four sites along British Columbia's outer coast (Hipfner and Galbraith 2013). Further, with one exception, in which mysids were the main prey type (O'Connell and Fives 1995), calanoid copepods were the primary prey of sand lances in all studies, so it was interesting that a more balanced array of prey, also including cladocerans, larvaceans, and teleosts, was taken in one of the three years of this study (1967).

The diet of the Pacific Sand Lance along British Columbia's outer coast included a broader array of copepod taxa and different life stages (Hipfner and Galbraith 2013) than in the Salish Sea (this study). *Pseudocalanus* (especially in the north) and *Calanus marshallae* (especially in the south) were the primary prey along the outer coast. *Pseudocalanus* was the primary prey in only one of the three years in the Salish Sea, and *C. marshallae* was not found at all. Copepod nauplii, the main prey of Pacific Sand Lance in two of the three years in the Salish Sea, occurred in trace amounts in just 2 of 12 site-years along the outer coast.

The differences between the two sets of studies could reflect any or all of four factors: (1) four decades separate them; (2) the age and size structure of the Pacific Sand Lance differed, with the outer coast study including only Pacific Sand Lance >100 mm fork length; (3) the timing of sampling differed (April to early July in the Salish Sea and July to early August along the outer coast); and (4) the copepod communities of the Salish Sea and the outer coast differ.

We cannot assess the role that changes in the marine environment over time may have played, but there is reason to believe that all three of the remaining factors were involved. First, sand lance diets vary with age and size (O'Connell and Fives 1995); for example, the amount of the larger *C. marshallae* consumed by Pacific Sand Lance increased with fork length, while the amount of the smaller *Pseudocalanus* did not (Hipfner and Galbraith 2013). Second, the fact that copepod nauplii (an early larval stage) were very common in diets in the Salish Sea in both years when sampling occurred in spring but not in any year in the Salish Sea or along the outer coast when sampling occurred in summer implies that seasonal timing is a factor. And lastly, the summertime copepod community of the Salish Sea is dominated by small copepods, including *Pseudocalanus* (Sastri and Dower 2009), which was the primary prey of Pacific Sand Lance in July 1966, whereas *Pseudocalanus* and *Calanus marshallae*, the dominant prey along the outer coast in all three years of study (2009, 2010, and 2011) (Hipfner and Galbraith 2013), are two of the three most abundant zooplankters in continental shelf waters from Oregon to the Bering Sea (Mackas and Coyle 2005).

Acknowledgements

We thank W. Barraclough, J. Fulton, and D. Robinson, all of the Fisheries Research Board of Canada, for conducting the trawl surveys (which were also funded by the Fisheries Research Board of Canada) in the 1960s, and we thank the students from the South Hampton Work Experience Program for transcribing their data. Thanks also to T. Gaston for commenting on a previous draft of the paper.

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Received 24 September 2013
Accepted 8 November 2013

Melanistic Diversity in the Maritime Gartersnake, *Thamnophis sirtalis pallidulus*, in Nova Scotia, Canada

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Gilhen, John, and Fred W. Scott. 2014. Melanistic diversity in the Maritime Gartersnake, *Thamnophis sirtalis pallidulus*, in Nova Scotia, Canada. Canadian Field-Naturalist 128(1): 63–71.

We describe an unusual diversity of melanistic conditions in populations of the Maritime Gartersnake, *Thamnophis sirtalis pallidulus*, in Nova Scotia: pure melanism, melanism, nigrismus (predominantly melanistic), abundismus (mosaic melanism). This variability is widespread in Nova Scotia, and it includes coastal islands.

Key Words: Maritime Gartersnake; *Thamnophis sirtalis pallidulus*; pure melanism; melanism; nigrismus; predominantly melanistic; abundismus; mosaic melanism; coastal islands; Nova Scotia

Introduction

Rowell (2012) explained that melanism is a Mendelian recessive trait that is rare or absent in most Common Gartersnake (*Thamnophis sirtalis*) populations. Peters (1964) and Klauber (1972) provide definitions of melanism, nigrismus, and abundismus. Melanism is an unusual increase in the normal amount of black pigment within a particular individual as contrasted with other members of his species. Occasionally used to characterize a species in which all individuals are equally black. Nigrismus is a type of melanism in which the specimen is not completely black and shows a change in the elements of the basic pattern as a consequence of an increase in the size of the black portion of the pattern, making the specimen predominantly black. Abundismus is a mosaic type of melanism in which the specimen is not completely black but shows a change in the elements of the basic pattern as a consequence of an increase in the number of black spots or blotches in the non-black areas of the pattern.

We propose a fourth type of melanism: pure melanism. The pure melanistic condition is uniform black on the back and does not show a spotted pattern when the skin is spread. This is the main character which separates the pure melanistic condition from the melanistic condition.

All four melanistic conditions are variable in the Maritime Gartersnake, *Thamnophis sirtalis pallidulus*, and are widespread in specimens found on the mainland, on Cape Breton Island, and on two coastal islands in Nova Scotia (Figure 1). In general terms, these melanistic conditions in the Maritime Gartersnake in Nova Scotia can be defined as follows.

Pure melanism

Individuals are a uniform satiny black to bluish-black on the back (Figure 2), rarely with purplish gleam. The back will be lustrous in some lights when the snake is freshly shed. The top of the head, the underside of the trunk, and the tail are glossy black to bluish-black, (like the melanistic condition, see the photograph on the cover). The infralabials, chin shields, and gular scales, are enamel white, rarely bright pinkish-white. The white shades change abruptly to black or bluish-black on the first few anterior ventral scales, and the black or bluish-black extends to the tip of the tail. The skin between the scales is dull dark grey to bluish-grey throughout. Only 4 specimens of the Maritime Gartersnake are known to manifest the pure melanistic condition (Table 1). They do not show a Maritime Gartersnake spotted pattern when the skin is spread.

Melanism

Individuals are usually satiny black to bluish–black on the back (Figure 3 before shedding and the same snake, see cover, two days after shedding), rarely with a purplish gleam. The back is lustrous in some lights, particularly when the snake is freshly shed. The top of the head and the underside of the trunk and tail are glossy black to bluish-black. The infralabials, chin shields, and gular scales can be enamel white, bluish-white, yellowish-cream, light orange (on snakes from Georges Island, Halifax County), and rarely pinkish-white. In addition, some individuals have black spots or streaks on the side of the jaw, the chin, and the throat. These light colours change abruptly to the darker ventral colour on the first few anterior ventral scales. The skin between the scales can be bluish-white, light grey, or light yellowish-brown. When the skin is spread, large ellipsoid-shaped spots or smaller alternating spots, and dorsal stripe, if present, (characteristic of the Maritime Gartersnake spotted pattern), are revealed. This pattern, when the skin is spread, is the most distinguishing character which separates it from the pure melanistic morph.

Counting the 3 young from Wellington, there are 27 records of the melanistic condition (Table 2) in Nova

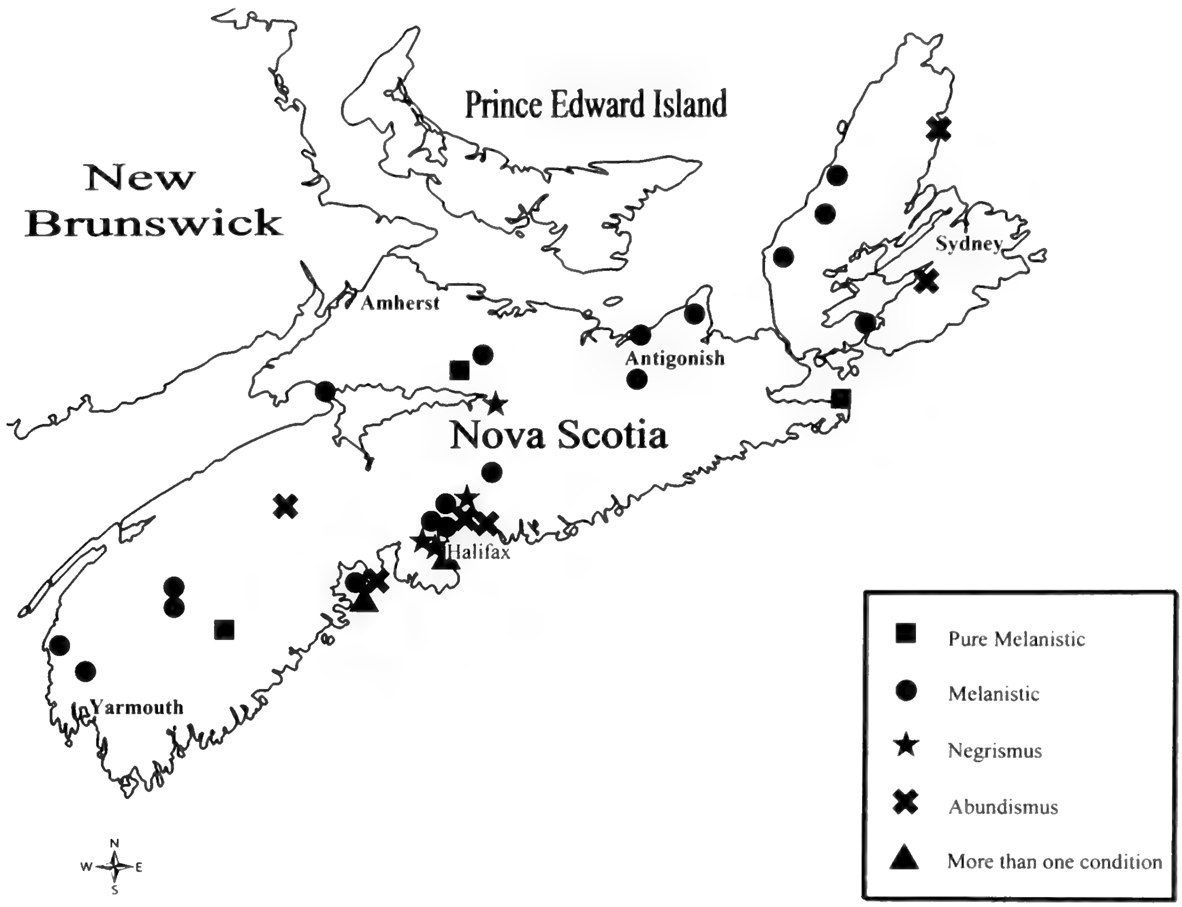

FIGURE 1. Distribution of the four melanistic conditions in the Maritime Gartersnake, *Thamnophis sirtalis pallidulus*, in Nova Scotia.

TABLE 1. Four pure melanistic Maritime Gartersnakes, (*Thamnophis sirtalis pallidulus*) from Nova Scotia, Canada, in chronological order.

Age	Sex	Locality	Date collected	Remarks
Adult	Female	Canso, Guysborough County	5 October 1905	Nova Scotia Museum, Piers no. 2937
Adult	Female	Lake Rossignal,Queens County	21 October 1970	Nova Scotia Museum970-Z-400-1 (Figure 2)
Adult	Female	Londonderry,Colchester County	24 May 1980	Sight record
Adult	Female	Big Tancook Island, Lunenburg County	18 August 2013	Anomaly. Brown labials, black ventral scales, and grey subcaudals (Figure 7)

Scotia; 11 of these reported observations were made from a distance and do not include a description of the underside of the body or tail.

Nigrismus or predominantly black

This is a type of melanism in which the individual looks uniform black from a distance and up close it is predominantly black. The spotted pattern, and dorsal stripe, when present, of a Maritime Gartersnake are black and the remaining ground colour is a mosaic of blackish clove-brown with scattered white scales (Gilhen 2000) (Figure 4). This morph is dark steel grey "plumbeous" to grey-black on the underside of the trunk and the tail (Figure 5). The underside of the tail of one individual was blackish clove-brown. The infralabials, chin shields, and gular scales may be bluish-white, or yellowish-cream to orange-cream, and may be freckled with grey. There are only four observations of the nigrismus or predominantly black condition in Nova Scotia (Table 3).

Abundismus or mosaic

In these Individuals, the normal spotted pattern is invaded by dark grey-black to black spots and/or blotch-

FIGURE 2. Pure melanistic Maritime Gartersnake, *Thamnophis sirtalis pallidulus*, from Lake Rossignol, Queens County, Nova Scotia, captured on 21 October 1970, by James Harding. Photo: R. Merrick.

FIGURE 3. Melanistic Maritime Gartersnake, *Thamnophis sirtalis pallidulus*, from Big Tancook Island, Mahone Bay, Lunenburg County, Nova Scotia, captured on 7 May 2012 (before it shed its skin). Photo: H. Dione

TABLE 2. Twenty- seven melanistic Maritime Gartersnakes (*Thamnophis sirtalis pallidulus*) from Nova Scotia, Canada, in chronological order.

Age	Sex	Locality	Date collected	Remarks
Unknown	Unknown	McNabs Island, Halifax County	13 May 1929	Nova Scotia Museum no. 6519. "from its colour it would be mistaken for a Black Snake (*Coluber constrictor*)"
Adult	Female	Fletcher 's Lake, Halifax County	15 July 1962	Sight record
Adult	Unknown	Jacques Landing, Queens County	16 August 1971	National Museum of Canada 13674. Park highway road kill.
Adult	Female	George 's Island, Halifax County	4 July 1991	Sight record
Adult	Female	George 's Island, Halifax County	23 July 1992	Sight record no. 1
Adult	Female	George 's Island, Halifax County	23 July 1992	Sight record no. 2. Dark brownish-black individual
Adult	Male	George 's Island, Halifax County	10 August 1992	Anomaly. Individual had Yellow dorsal stripe anteriorly (Figure 8)
3 Young	Unknown	Wellington, Yarmouth County	27 June 1995	F. R. Cook field numbers 18758, 18762 and stillborn 18771
Unknown	Unknown	Mull River, Inverness County	16 May 1999	Nova Scotia Herpetological Atlas no. 3679
Unknown	Unknown	Upper Margaree, Inverness County	10 June 1999	Nova Scotia Herpetological Atlas no. 10072
Unknown	Unknown	Margaree Forks, Inverness County	10 June 1999	Nova Scotia Herpetological Atlas no. 11900
Unknown	Unknown	Margaree Forks, Inverness County	11 June 1999	Nova Scotia Herpetological Atlas no. 10073
Unknown	Unknown	Clark Lake, Colchester County	25 July 2000	Nova Scotia Herpetological Atlas no. 4352
Unknown	Unknown	Ponds, Pictou County	15 August 2000	Nova Scotia Herpetological Atlas no. 4883
Adult	Female	Dilligent River, Cumberland County	3 July 2002	Nova Scotia Herpetological Atlas no. 9196
Unknown	Unknown	Timberlea, Halifax County	August 2002	Remains of house cat kill
Unknown	Unknown	Sampsonville, Richmond County	12 October 2002	Nova Scotia Herpetological Atlas no. 10000
Adult	Female	Fairmont Road, Antigonish County	9 June 2003	Nova Scotia Herpetological Atlas no. 10451
Adult	Female	Grafton Lake, Queens County	10 July 2003	Sight record. Individual had bluish stripes
Unknown	Unknown	Gamble Lake, Colchester County	6 July 2004	Sight record
Adult	Female	Dilligent River, Cumberland County	12 August 2004	Nova Scotia Museum catalogue no. 55514
Adult	Female	Argyle Sound, Yarmouth County	Summer 2004	Nova Scotia Museum catalogue no. 55593
Adult	Female	Garden of Eden, Pictou County	4 July 2008	Sight record. Individual near shedding, blue eyes
Adult	Female	Big Tancook Island, Lunenburg County	7 May 2012	Individual has bluish stripes
Adult	Female	Lake Doucette, Digby County	30 September 2012	Nova Scotia Museum catalogue no. 55587

FIGURE 4. Dorsal view of nigrismus Maritime Gartersnake, *Thamnophis sirtalis pallidulus*, from McCabe Lake, Halifax County, Nova Scotia, captured on 24 June 1969. See also Figure 5. Photo: J. Gilhen.

FIGURE 5. Ventral view of the nigrismus Maritime Gartersnake, *Thamnophis sirtalis pallidulus*, shown in Figure 4. Photo: J. Gilhen.

es (Figure 6). The spots may be small, and involve only a few scales on one side, may be large and invasive of the dorsal spotted pattern and stripe, or may involve just the underside of the trunk and tail. The remaining ground colour or pattern is as variable as any Maritime Gartersnake in Nova Scotia. There are 9 records of the abundismus condition (Table 4). Abundismus individuals are often referred to in Nova Scotia as part-melanistic.

TABLE 3. Four nigrismus Maritime Gartersnakes (*Thamnophis sirtalis pallidulus*) from Nova Scotia, Canada, in chronological order.

Age	Sex	Locality	Date collected	Remarks
Adult	Unknown	Paddy Lonis Brook, Halifax County	29 April 1918	Nova Scotia Museum catalogue no. 4604
Adult	Female	Withrod Lake, Halifax County	6 May 1934	Nova Scotia Museum catalogue no. 7783
Unknown	Unknown	Mill Brook, Colchester County	7 August 1935	Nova Scotia Museum Catalogue no. 8224
Adult	Female	McCabe Lake, Halifax County	24 June 1969	Canadian Museum of Nature Amphibians and Reptiles no.12153 (Figures 4 and 5)

TABLE 4. Nine abundismus Maritime Gartersnakes (*Thamnophis sirtalis pallidulus*) from Nova Scotia, Canada, in chronological order.

Age	Sex	Locality	Date collected	Remarks
Adult	Male	Tomahawk Lake, Halifax County	5 July 1970	Site record
Unknown	Unknown	Big Pond, Cape Breton County	17 August 1977	National Museums of Canada NMCAR25368
Adult	Male	George 's Island, Halifax County	26 May 1989	Sight record no. 1 (see Figure 6)
Adult	Male	Georges Island, Halifax County	26 May 1989	Sight record no. 2
Adult	Male	George's Island, Halifax County	14 April 1992	Sight record
Adult	Male	George's Island, Halifax County	11 May 1992	Sight record
Adult	Male	South Ingonish beach, Victoria County	5 September 1996	Nova Scotia Museum 55056
Adult	Male	Big Tancook Island, Lunenburg County	24 May 2003	Sight record
Adult	Male	Mack Lake, Kings County	23 August 2003	Nova Scotia Museum 55592

FIGURE 6. Abundismus Maritime Gartersnake, *Thamnophis sirtalis pallidulus*, from Georges Island, Halifax Harbour, Halifax County, Nova Scotia, captured on 26 May 1989. Photo: J. Gilhen.

Discussion

For almost a century and a half, there have been published and oral reports of black snakes from Nova Scotia, New Brunswick, and Prince Edward Island (Bleakney 1958). John Matthew Jones (1865) published the first list of amphibians and reptiles of Nova Scotia and he included the Black Snake, *Coluber constrictor* (i.e., North American Racer). Gilpin (1875) also gives an account of the Black Snake. These reports of the Black Snake, *C. constrictor*, are believed to be in error and actually can be attributed to the melanistic morph of the Maritime Gartersnake, as indicated by Harry Piers (Gilhen 2000) and mentioned by Bleakney (1958), Cook (1967), and Gilhen (1984). The North American Racer and North American gartersnakes (*Thamnophis spp.*) are easily distinguished from one another by the scales on their back. The North American Racer has smooth dorsal scales and North American gartersnakes have strongly keeled scales.

The 4 melanistic conditions described above are uncommon in Nova Scotia but widespread. The ratio of melanistic individuals to four other recognized colour patterns in wild populations in Nova Scotia is not known. Only Georges Island, Halifax County, was surveyed specifically for Maritime Gartersnakes (Barnes *et al.* 2006). Between May and October 1993, a total of 391 Maritime Gartersnakes were marked on this 5-ha drumlin in Halifax Harbour. Barnes *et al.* (2006) state, "Rarely were individuals melanistic (solid black) or partially melanistic (five individuals)."

Over 100 Maritime Gartersnakes have been observed on Big Tancook Island by JG but only 3 individuals — one pure melanistic anomaly, one melanistic, and one abundismus were observed and photographed. We have kept 6 melanistic females from various localities until they gave birth, but they did not produce melanistic young. We have observed more than 20 non-melanistic females from various localities in Nova Scotia give birth, and none of their young were melanistic. Also, we have not found melanistic young in the field. However, Francis R. Cook collected two non-melanistic pregnant females from Wellington, Yarmouth County, one on 27 June 1995 and the second on 2 July 1995. Both females gave birth in captivity. The female from 27 June, gave birth to 16 young (3 melanistic and 13 non-melanistic). The female from 2 July gave birth to 13 normal young. During annual visits from 1963 to 1995 to the former Frank Crosby farm at Wellington,

Francis R. Cook and Joyce Cook never saw a melanistic Maritime Gartersnake. Also, Joyce Cook lived there from 1948 to 1958 and did not see a melanistic snake, nor were any noted by her parents or two brothers.

Melanism is more common in the Eastern Gartersnake, *Thamnophis sirtalis sirtalis*. Rowell (2012) provides a table (Table 24.1) listing the incidence of melanism reported at locations in southern Ontario, particularly on islands of western Lake Erie and at nearby mainland locations. The incidence varied from 6.4% at Point Pelee to 12%–59% at Point Pelee Island, East Sister Island, and Middle Island, and 24%–51.2% at Long Point.

Pure melanistic

The first recorded observation of pure melanism in a Maritime Gartersnake is by Harry Piers (Accession Book No. 1, Nova Scotia Museum no. 2937). He stated, "Melanistic variety of Common Garter Snake, All Saints Rectory grounds, Canso, Guysborough County, by Rev. R. M. Leigh's man on 5 October 1905". Under Remarks he stated "Colour. – Back black, with no sign whatever, in any light, of blotches or stripes, etc.; underside of head white; belly slate-coloured, the under plates (belly & tail) narrowly margined with lighter. Ventral plates with a black spot on outer margin, near beginning of dorsal scales, thus being almost concealed by the next ventral plate."

A large female from Londonderry was most unusual in that it was black with a distinct purplish lustre. The infralabial scales, chin shields, gular scales, and first few ventral scales were glossy pinkish-white and the remaining underside was grey-black with a pinkish lustre. The large female from Big Tancook Island was different and unusual in that the supra-labials and neck were brown fading to yellowish-cream on the infralabials, chin shields, gular scales, and first few ventral scales. This snake had a light lateral stripe on both sides anteriorly. The belly was black nearly to the anal plate and then changed abruptly to grey to the tip of the tail (Figure 7). It resembled mostly the pure melanistic condition. When the skin was spread, a Maritime Gartersnake spotted pattern was not revealed.

Melanistic

The first recorded observation of melanism in a Maritime Gartersnake is by Harry Piers (Accession Book No. 3, Nova Scotia Museum no. 6519). He recorded a

Figure 7. Adult male melanistic Maritime Gartersnake, *Thamnophis sirtalis pallidulus*, anomaly with light yellow anterior dorsal stripe from Georges Island, Halifax County, Nova Scotia, captured on 10 August 1992. Photo: J. Gilhen.

"Striped Garter Snake ABNORMAL MELANISTIC INDIVIDUAL!!" from McNab's Island, Halifax Harbour, Halifax County, captured on 13 May 1929 by Joseph Perrin. "From its colour it would be mistaken for a Black Snake (*Coluber constrictor*)" (i.e., North American Racer). This may be the same variation of melanism exhibited by a female from Grafton Lake, Queens County, on 10 July 2003 and a female from Big Tancook Island, Lunenburg County, on 3 October 2011. Both females had blue-black dorsal and lateral stripes.

Of the 27 Maritime Gartersnakes reported here as melanistic, 9 were reported in the Nova Scotia Herpetological Atlas (NSHA). Since a description and/or image was not given, the Nova Scotia Herpetological Atlas number for each one is provided in Table 2.

The underside of the snake from Garden of Eden was not recorded and its blue eyes indicate it was about to shed. Two rare variations and one anomaly were found in the melanistic condition on Georges Island. One individual was dark brownish-black with orange at the corner of the mouth fading to yellowish-white on the chin and extending onto the first few ventral scales. Another snake from Georges Island was similar to a large pure melanistic female from Londonderry in that it was black with a distinct purplish gleam (Barnes *et al.* 2006.). The chin and first few ventral scales were glossy pinkish-white and the remaining underside was dark pinkish-grey. One snake from Timberlea, Halifax County, was dark blueberry-blue on the back. The underside of the trunk was bluish-black. The sides of the head were blue fading to bluish-white on the chin shields. One adult male anomaly had a light yellow dorsal stripe anteriorly (Figure 8).

Nigrismus

The first recorded observation of nigrismus in a Maritime Gartersnake is also by Harry Piers (Accession Book No. 2, Nova Scotia Museum no. 4604). He recorded a striped garter snake, with melanistic tendency from Paddy Lonis Brook, one mile SSE of Enfield, Halifax County, on 29 April 1918. His detailed account of the colour is as follows: "Colour from fresh specimen. General colour very dark; stripes moderately plain (on anterior parts; spots very obscure owing to dark colour of back. Top of head and back blackish, Clove-Brown. Upper labials and lower part of snout plate (rostral) Buff. Iris, brown. Dorsal stripe (on dorsal row of scales and part of row on each side of it), dirty white; plainest for about 5 inches back of snout, and becoming lost about 12 ½ inches behind snout (that is, a little more than half-way of length). The stripe is broken for a couple of inches behind the head by the connection across it of 5 of the dark spots on each side of it. Lateral stripe on parts of 2nd and 3rd rows of scales pale olive-buff, plainest for about 5 inches behind snout, not so evident or so light as the dorsal stripe, and becoming lost about

FIGURE 8. Pure melanistic Maritime Gartesnake, *Thamnophis sirtalios pallidulus*, anomaly with yellowish-brown supralabials fading to yellowish-white on underside of head and with blackish ventral scales and greyish subcaudal scales, from Big Tancook Island, Lunenburg County, Nova Scotia, captured on 18 August 2013. Photo: R. Lloyd.

anus (about 17 inches from snout). Two rows of obscure black spots, the inner row about .10 inch diameter each spot, the outer row about .15 inch diameter each spot, arranged alternately (zig-zag fashion) on each side of dorsal stripe (that is between dorsal stripe and lateral stripe); these spots somewhat noticeable for 4 or 5 inches behind snout, but soon become lost in the general blackish colour of upper parts. Underside of head, bluish-white. Belly and underside of tail plumbous, the abdominal plates each with a black spot on the front lateral part. "

Abundismus

Abundismus or the mosaic condition is extremely variable. All 9 individuals recorded differed in the amount of black pigment. The spots can be small and involve only a few scales, large patches, or extensive grey-black areas, particularly on the posterior half of the body and tail, and the spots or areas invade or cover the normal spotted pattern and stripes (Figure 6).

Acknowledgements

We thank Francis R. Cook, Curator Emeritus and Research Associate, Canadian Museum of Nature, for his encouragement, and for prodding JG over many years to complete the manuscript. Dr. Cook and Andrew Hebda, Curator of Zoology, Nova Scotia Museum of Natural History, pre-reviewed and made useful comments on the manuscript. We are grateful to the following persons who either collected or provided reports of Nova Scotia Maritime Gartersnakes in a melanistic condition: David Baker, Joseph Baker, Suzanne Barnes, Francis R. Cook, James Callaghan, Gary Corbett, Stan Corbett, Albert d'Entremont, Hillary Dione, Gert Ewelt (Nova Scotia Herpetological Atlas no. 4883), Calvin Fraser, Karen Gilhen, Michael Gilhen, David Gordon, May Goring, Ross Hall (Nova Scotia Herpetological Atlas no. 4352), Anne-Belle Hamilton, James Harding, David E. Harris, Peter Hope, Andrew Kennedy, Randy Lauff, Earl Luffman, George MacInnis, Norman Maloney, Mike McCabe, Ronald Merrick, John Mills (Nova Scotia Herpetological Atlas nos. 10072, 10073, and 11900), Dana Pierce, Russell Rogerson, and Wayne F. Weller. We thank Jeffrey Rowell for permission to cite his privately printed book on the snakes of Ontario.

Roger Lloyd, photographer, Nova Scotia Museum, developed digital images of all melanistic Maritime Gartersnakes from original colour transparencies and pictures taken by Ronald Merrick, JG, and Hillary Dione. The cover image is by Roger Lloyd. We thank naturalists Graham Caswell, Mary MacDonald, and Heather McKinnon for the professional care of the live Maritime Gartersnake display in the Netukulimk Gallery, giving us ample opportunity to study and photograph Maritime Gartersnakes in melanistic conditions. Kim Franklin, administrative assistant, and Roger Lloyd assisted in the development of Tables 1–4.

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Received 27 September 2013
Accepted 18 November 2013

Notes

Thickness of Common Murre (*Uria aalge*) Eggshells in Atlantic Canada

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Pirie-Hay, Donald W., and Alexander L. Bond. 2014. Thickness of Common Murre (*Uria aalge*) eggshells in Atlantic Canada. Canadian Field-Naturalist 128(1): 72–76.

Reported values for eggshell thickness in Common Murre (*Uria aalge*) are few, and even fewer since the decline in use of organochlorine pesticides and other environmental pollutants that caused significant thinning of shells. The eggshells of Common Murres and Thick-billed Murres (*Uria lomvia*) are among the thickest and heaviest, proportionately, of any bird and this represents a non-trivial maternal investment. We measured the length and breadth of Common Murre eggs collected from Machias Seal Island, New Brunswick, in 2006, and Gull Island, Newfoundland and Labrador, in 2012, and we measured the thickness of the eggshells. Shell thickness was not related to egg size or volume, and it varied in individual eggs. The shells of Common Murre eggs from Machias Seal Island (mean and standard deviation [SD] (0.767, SD 0.078 mm) and Gull Island (0.753, SD 0.057 mm) were significantly thicker than any previously reported value and among the thickest of all birds. Such thickness is likely a result of nesting on rock substrate with no nesting material and, perhaps, high breeding densities.

Key Words: Common Murre; *Uria aalge*; eggshell thickness; egg size; Atlantic Canada; Bay of Fundy; Gull Island; Machias Seal Island; Witless Bay; New Brunswick; Newfoundland and Labrador

Introduction

The integrity of avian eggshells, which are composed mainly of calcium carbonate, is critical for successful breeding (Gill 2007). Eggshell thickness depends on the dietary intake of calcium of the egg-laying female (Uspenski 1958); thus, the need to produce thick shells creates high calcium demand. Thickness is also affected by organochlorine pesticides, introduced in the 1940s. These compounds caused widespread eggshell thinning in birds (Bitman *et al.* 1969; Ratcliffe 1970; Lundholm 1997), and the most detrimental, dichlorodiphenyltrichloroethane (DDT), was banned in North America in the 1970s.

Common Murres (*Uria aalge*) are cliff-nesting seabirds that typically breed in high-density colonies (Tuck 1961). They build no nest. The shells of their ovate-pyriform to elliptical-ovate eggs are thicker at the narrow end, a characteristic shared with Razorbills (*Alca torda*) and presumably an adaptation to nesting on bare rock (Belopolskii 1961; Ainley *et al.* 2002). Given the conditions of the nesting habitat, thick shells prevent egg loss and breakage and, therefore, thickness is an important factor in breeding success. The shape of Common Murre eggs is adapted to maximize the surface area in contact with the brood patch to facilitate incubation (Harris and Birkhead 1985; Ainley *et al.* 2002), and the small roll radius, which further decreases as the egg develops, helps prevent the egg from rolling off the ledge (Uspenski 1958). Murres, along with penguins (Spheniscidae), cormorants (Phalacrocoracidae), and guillemots (Alcidae: *Cepphus* spp.), have the heaviest eggshells relative to whole egg mass of any flying bird (Schönwetter 1960-1992).

The purpose of our study was to determine eggshell thickness and its relation to egg size of Common Murres in contemporary samples from two sites in Atlantic Canada and to compare eggshell thickness with previously published values. We also investigated the relation between eggshell thickness and other physical characteristics (colour and speckling pattern).

Methods

We collected Common Murre eggs from two sites in Atlantic Canada: Machias Seal Island, New Brunswick (44°30'N, 67°06'W), where about 100 pairs of Common Murre breed beneath large boulders (Diamond and Devlin 2003; Bond and Diamond 2006) and Gull Island (47°16'N, 52°46'W) in the Witless Bay Ecological Reserve, Newfoundland and Labrador, which supports approximately 10 000 breeding pairs of Common Murres (S. I. Wilhelm, Canadian Wildlife Service, unpublished data, 2012).

We collected 10 whole eggs from Machias Seal Island in June 2006 and 69 intact and partly broken shells from eggs depredated by gulls (*Larus* spp.) on Gull Island in July 2012. Because gulls could be targeting younger inexperienced breeders, which have thinner eggshells (Hipfner *et al.* 2003), we also collected 20 eggs from known established breeders near the centre of nesting cliffs on Gull Island in June 2013.

For mostly intact eggs from Gull Island, eggshell thickness (including the egg membrane) was measured at six locations: four equidistant points at the equator (i.e., largest circumference) and one at each end of the egg. Thickness was measured to the nearest 0.0025 mm using a spring-loaded micrometer. Measurements at

the ends of the eggs were taken on the flattest part to avoid measuring a strongly curved surface, especially at the narrow end. Any obvious exterior or interior surface or shell irregularities were avoided. Average thickness of the egg membrane was determined by measuring the difference in shell thickness with and without the membrane at a sample of adjacent spots on the egg ($n = 10$, selected randomly from all eggs). The mean of the four thickness measurements at the equator (minus mean egg membrane thickness) was recorded as middle eggshell thickness. We assessed measurement error by measuring 21 eggs twice on different days. A single observer made all measurements.

We measured the length and breadth of intact eggshells ($n = 50$ from Gull Island, not including any collected in 2013) with dial callipers, to the nearest 0.1 mm. Because eggs were depredated by gulls, both measurements could not be made on all eggs (breadth $n = 44$, length $n = 40$). Ground colour and speckling pattern of eggs were sorted into one of five classes, as defined by Gaston and Nettleship (1981), with higher numbers indicating more base and speckling pigmentation in the eggs. As depredated eggs might be more likely to come from young or inexperienced females and, therefore, have thinner shells (Hipfner *et al.* 1999), eggshell thickness measurements from Gull Island in 2012 should be taken as a minimum estimate.

Statistical methods

We used repeated-measures analysis of variance (ANOVA) to examine within-egg variation in shell thickness between the bottom (round end), middle (largest circumference), and top (narrow end) of eggs collected from Gull Island in 2012. Only eggs with measurements for all locations were included.

We used Tukey's honest significant difference (HSD) post-hoc test for pairwise comparisons. To determine whether shell thickness at the top (the measurement with the largest sample size, $n = 58$) increased with increasing ground colour and speckling pattern, we used Kruskal-Wallis rank-sum test.

We tested relations between egg size (length, breadth, and volume) and shell thickness using linear regression. A volume index was calculated as length × breadth^2 (Hipfner and Gaston 1999).

Finally, we compared the thickness of our shell samples with previously published values (Gress *et al.* 1971; Henny *et al.* 1982; Pyle *et al.* 1999; Zimmerman and Hipfner 2007) and tested differences using ANOVA and Tukey's HSD. All tests were performed in R 3.0.2 (R Development Core Team 2013), and differences were considered significant when $P < 0.05$. Data are presented as the mean and standard deviation (SD).

Results

Differences between repeated measurements of the thickness of the same shells were small (0.016, SD 0.021 mm) and ranged from zero to 0.145 mm or 0.0–8.6% of shell thickness. The membrane measured 0.070 mm (SD 0.049), or 8.2% of the combined thickness of the shell and membrane. Among the 21 eggs assessed twice on different days, categorization of ground colour and speckling pattern differed for two and five eggs, respectively; in all cases, the assessment differed in a single category.

Shell thickness varied within each egg at both sites (Table 1). At Gull Island in 2012, repeated measures (ANOVA, $F_{2,44} = 310.3$; $P < 0.001$) showed that the mean thickness of the shell at the bottom (0.687, SD 0.066 mm) was thinner than at the middle (0.753, SD 0.057 mm, $P < 0.001$), and the mean thickness of the shell at the middle was thinner than at the top (0.906, SD 0.062 mm, $P < 0.001$). We observed a similar pattern in shells from Machias Seal Island (repeated meas-

TABLE 1. Shell thickness and size of Common Murre (*Uria aalge*) eggs from Gull Island, Newfoundland and Labrador (2012) and Machias Seal Island, New Brunswick (2006).

Shell thickness	*n*	Range (mm)	Mean (mm)	SD (mm)
Gull Island				
Top	58	0.761–1.040	0.906	0.062
Middle*	56	0.664–0.822	0.753	0.057
Bottom	54	0.568–0.860	0.687	0.066
Machias Seal Island				
Top	9	0.780–0.932	0.829	0.058
Middle*	8	0.726–0.907	0.767	0.078
Bottom	7	0.653–0.866	0.684	0.064
Egg size				
Gull Island				
Length	40	74.2–90.8	82.2	3.6
Breadth†	44	47.6–53.9	50.7	1.4
Machias Seal Island				
Length	10	79.0–91.0	84.6	3.3
Breadth†	10	49.4–52.9	50.0	3.5

*At the "equator" or largest circumference.

†Largest diameter.

ures ANOVA, $F_{2,8}$ = 9.29, P = 0.008); although the mean thickness of the shell at the top and at the middle did not differ (P > 0.05), both were thicker than at the bottom (P < 0.05). On Gull Island, mean shell thickness in 2012 did not vary with ground colour (χ^2 = −1.91, df = 4, P = 0.75) or speckling pattern (χ^2 = −1.31, df = 4, P = 0.86; Table 2).

The mean length and mean diameter of Gull Island eggs in 2012 were 82.2 mm (SD 3.7) and 50.7 mm (SD 1.4), respectively; these measures for Machias Seal Island eggs were 84.6 mm (SD 3.3) and 50.0 mm (SD 3.5). At both sites, there was no detectable correlation between eggshell thickness at the six measured locations and length (all P > 0.08 and r^2 < 0.08), diameter (all P > 0.23 and r^2 < 0.04), or volume index (all P > 0.58, and r^2 < 0.01).

Common Murre eggs collected from Gull Island in 2012 and Machias Seal Island in 2006 were significantly thicker than any previously reported value ($F_{8,283}$ = 57.55, all pairwise comparisons P < 0.05; range of means: 0.54–0.716 mm; Figure 1). The mean thickness of the shells of the 20 eggs collected from known established breeders on Gull Island in 2013 was significantly greater than the mean thickness of eggshells measured in 2012 on Gull Island (middle: 0.811, SD 0.040 mm, P < 0.001), but was not significantly greater than the mean thickness of eggshells on Machias Seal Island (middle: 0.767, SD 0.078 mm, P = 0.58).

TABLE 2. Ground colour and speckle pattern on Common Murre (*Uria aalge*) eggs from Gull Island, Newfoundland and Labrador (2012).

Ground colour	No. of eggs
Class 1 (lighter)	14
Class 2	23
Class 3	12
Class 4	10
Class 5 (darker)	7
Unclassified	3
Speckle pattern	
Black speckles with blotches at large end	14
Brown spots with a few scribbles	4
Faint brown scribbles	7
Black scribbles	18
Black blotches	24
Unclassified	2

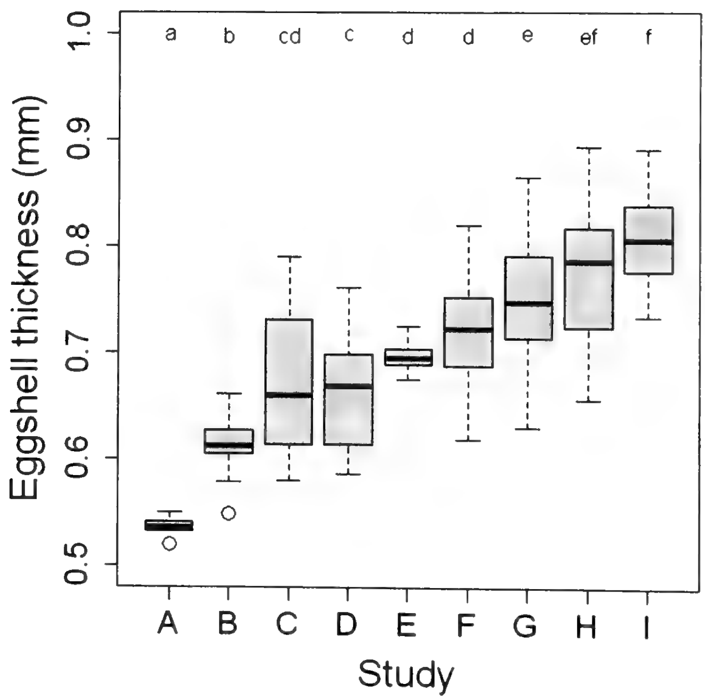

FIGURE 1. Shell thickness at the equator of Common Murre eggs in Atlantic Canada (G–I) compared with that reported in other studies (A–F). Groups not sharing the same lowercase letter above are significantly different (Tukey's HSD, P < 0.05). Black horizontal lines indicate the mean, shaded boxes are the first and third quartiles, whiskers are the 5–95% data range, and open dots are extremes. A, Triangle Island, British Colombia (Zimmerman and Hipfner 2007); B, Farallon Islands, California, 1968 and 1970 (Gress *et al.* 1971); C, Island Rock and Gull Island, Oregon, 1979 (Henny *et al.* 1982); D, Southeast Farallon Island and Ano Nuevo Island, California, 1993 (Pyle *et al.* 1999); E, Farallon Islands, California, 1913 (Gress *et al* 1971); F, Pacific Coast, northern California to Queen Charlotte Islands, British Columbia, pre-1947 (Henny *et al.* 1982); G, Gull Island, Newfoundland and Labrador, 2012; H, Machias Seal Island, New Brunswick, 2006; and I, Gull Island, 2013.

Discussion

Like those of Thick-billed Murres (Uspenski 1958), eggs of Common Murres are not of uniform thickness. Greater thickness at the top allows the egg to withstand the same amount of pressure there as at the bottom, but over a smaller surface area. Egg size was not related to shell thickness at any location on the egg, nor was there any relation between thickness and level of pigmentation.

The eggs collected in Atlantic Canada had the thickest shells ever recorded for Common Murres. In the comparison, we excluded eggs measured at Gull Island in 1977 and 1978 (0.43 mm, measured by vapour conductance; Mahoney and Threlfall 1981), because they were measured by a different method: vapour conductance.

The only other record of shell thickness after the rapid decline in use of organochlorine pesticides (Zimmerman and Hipfner 2007) also differs significantly from our measurements. These eggs, collected from Triangle Island, British Columbia, had a lower average shell thickness (0.54, SD 0.005 mm), but egg length (85.5, SD 3.5 mm) and diameter (50.5, SD 1.2 mm) were similar despite a small sample size (n = 6 for thickness, n = 15 for length and breadth; Zimmerman and Hipfner 2007). The thicker eggshells in the Atlantic region suggest population differences between the two oceans, where birds are known to experience different ecological pressures (Ainley *et al.* 2002). Differences in contemporary eggshell thickness could be related to salinity (Dyck and Kraul 1984) or the availability of calcium in pre-breeding diets (Bientema *et al.* 1997; Brenninkmeijer *et al.* 1997).

Our study is the first to examine the relation between egg size and shell thickness in this species. Although we found no such relation, this is the first investigation of its kind among Common Murres, and similar research is recommended at other colonies, particularly those where shell thinning is known to have occurred as a result of environmental pollutants.

Williams *et al.* (1982) found that, among Charadriiformes, eggshell mass, as a proportion of total egg mass, is highest among murres (13.7% for Common Murres and 14.4% for Thick-billed Murres), compared with terns (Sternidae: 4.8–10.7%) and gulls (*Larus* spp.: 5.9–11.8%); this progression corresponds to decreasing rigidity of nest sites (bare rock [murres], sand and gravel [terns], and plant material [gulls], Williams *et al.* 1982). Penguins, cormorants, and murres have the heaviest proportional eggshells among seabirds (Williams et al. 1982). Although Razorbills (*Alca torda*) nest on substrates similar to those used by Common Murres, they aggregate much less densely (Birkhead 1978), and their eggshells are proportionally less massive (8.66 ± 0.36%; Birkhead and Nettleship 1984). It is possible that species breeding on a rigid breeding substrate without nesting material and in dense aggregations (relative to other seabirds) combine to produce some of the relatively thickest and heaviest eggshells.

Conclusions

Our results show that Common Murres from Atlantic Canada have the thickest eggshells recorded for this species and that even the eggshells of supposedly inexperienced breeders are thicker than those found elsewhere. Thickness varied with location on the egg, and thickness was not related to egg size or volume. Eggs of established breeders had thicker shells than those depredated by gulls, possibly produced by younger murres. This is one of only a few studies to investigate eggshell thickness in seabirds since the decline of organochlorine pesticide use. We recommend further research to investigate contemporary murre eggshell thickness throughout the breeding range and possible ecological, toxicological, or phylogenetic influences.

Acknowledgements

We thank the Canadian Coast Guard and Canadian Wildlife Service for permission to work on Machias Seal Island and the Parks and Natural Areas Division of the Newfoundland and Labrador Department of Environment and Conservation for permission to work in the Witless Bay Seabird Ecological Reserve. Collections were made with permission of the Canadian Wildlife Service (permits ST 2455, SS 2784), and whole eggs were collected with the approval of the University of New Brunswick Animal Care Committee (protocol 06032). Environment Canada, the Atlantic Cooperative Wildlife Research Network, the Science Horizons Youth Internship Program, Collaborative Mercury Research Network, and the Natural Sciences and Engineering Research Council of Canada provided financial support. We thank G. M. Bouchard, T. C. Clarke, A. W. Diamond, and A. Patterson (Bold Coast Charter Co., Cutler, Maine) for logistic and field support in New Brunswick and K. A. Hobson, G. J. Robertson, S. I. Wilhelm, the Canadian Wildlife Service, and Environment Canada for logistic support in Newfoundland. Comments from A. J. Gaston, G. J. Robertson, and an anonymous reviewer improved previous drafts of this manuscript.

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Received 1 April 2013
Accepted 30 August 2013

The Most Northerly Black Witch (*Ascalapha odorata*): A Tropical Moth in the Canadian Arctic

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Ekrem, Torbjørn, Peter G. Kevan, Thomas S. Woodcock, and Paul D. N. Hebert. 2014. The most northerly Black Witch (*Ascalapha odorata*): a tropical moth in the Canadian Arctic. Canadian Field-Naturalist 128(1): 77–79.

A specimen of the Black Witch (*Ascalapha odorata*) was collected in August 2006 near Churchill, Manitoba, at 58.7652°N. This represents the most northerly record for this species. DNA barcode comparison of 93 specimens of *A. odorata* in the Barcode of Life Data Systems revealed low genetic divergence even though these specimens were collected from a large geographical area. The haplotype of the Churchill specimen was shared by only one other individual (collected in the Yucatán Peninsula of Mexico) in the Barcode of Life Data Systems. A definite assignment of the geographic origin of the Churchill specimen is not possible with current data, but more extensive analysis of Central American populations with additional genetic markers might resolve this uncertainty.

Key Words: Black Witch; Mariposa de la muerte; *Ascalapha odorata*; DNA barcoding; distribution; genetic divergence; migratory; migration; Manitoba

Ascalapha odorata (Linnaeus) (Black Witch) is one of the largest members of the superfamily Noctuoidea in North America. Although it has been collected from Canada to Argentina and even from Hawaii (Quinn 2008–2014*) (Figure 1), the natural breeding range of *A. odorata* is thought to be limited to Central America and the southernmost United States, including Texas and Florida (Wagner *et al*. 2011; Quinn 2008–2014*).

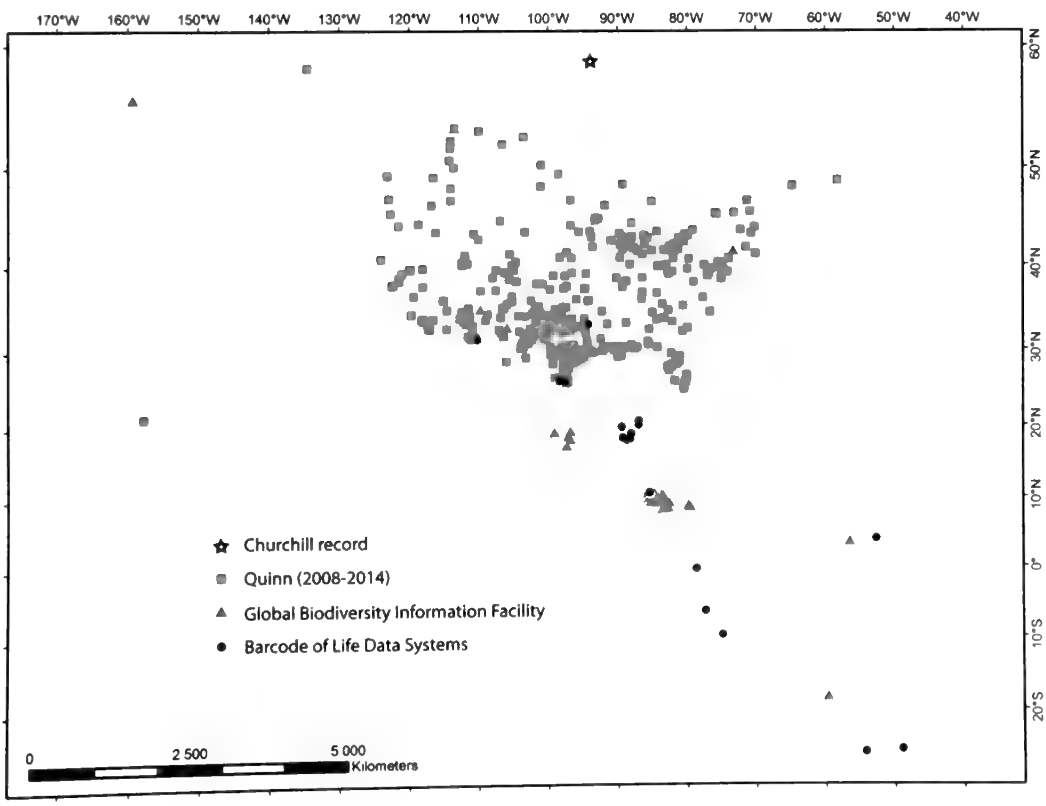

FIGURE 1. Collection sites of specimens of *Ascalapha odorata* (Black Witch) currently registered in the Barcode of Life Data Systems (black dots, star), the Global Biodiversity Information Facility (red triangles), and by Quinn (2008–2014*) (orange squares), accessed January 2014, most northerly observed record from Bird Cove, 18 km east of Churchill (star).

The caterpillars of the Black Witch have also been observed on introduced acacias in the greater Los Angeles area (Wagner *et al.* 2011).

This moth is a seasonal migrant to more northerly regions of North America. Most Canadian records are from summer and early autumn. Quinn (2008–2014*) gives an excellent summary of records from the United States and Canada, and several additional records are available through the Global Biodiversity Information Facility (http://www.gbif.org). These are shown in Figure 1. Additional North American sightings can be seen in the Butterflies and Moths of North America website (Opler *et al.* 2013*) and the North American Moth Photographers Group website (North American Moth Photographers Group 2014*), although many of these records are the same as those reported by Quinn (2008–2014*).

Most past Canadian records derive from sites in southern Canada, but specimens have a broad longitudinal distribution, with records from Newfoundland to British Columbia. In 2012 there were particularly frequent incursions of this moth into Canada (Quinn 2008–2014*).

The species also appears to engage in southerly and altitudinal migrations, as specimens are known from as far south as Argentina and into Andean locales (Henderson 2002). Its broad dispersal to temperate and high-elevation sites may reflect migratory flights to cooler environments, as is known for a number of other noctuoids (Kevan and Kendall 1997).

Ascalapha odorata is a recurring visitor to Canada, but most past records have been restricted to southern regions of the country. Although one of its larval host plants, *Gymnocladus dioicus* (Kentucky Coffee-tree), is native to Carolinian Canada and adult food resources of over-ripe fruit (e.g., *Prunus* spp.) are widespread in Canada, this species is unlikely to become established, as all life stages are believed to be intolerant to prolonged freezes (Wagner *et al.* 2011).

The primary motivation for this paper lies in reporting the discovery of a live female *Ascalapha odorata* on 18 August 2006 resting on *Empetrum nigrum* (Black Crowberry) at Bird Cove, a rocky headland on Hudson Bay about 18 km east of Churchill, Manitoba (58.7652°N, 93.8682°W) (Figure 2). This specimen represents the most northerly record for any Black Witch, displacing the previous record holder, a specimen collected at Auke Bay, 13 km north of Juneau, Alaska (58.3833°N, 134.5822°W) (Spangler 1957).

The Churchill specimen is the first individual of *A. odorata* found in the Low Arctic tundra. This individual probably arrived in the Hudson Bay area on strong southerly winds about a week before its discovery (P. Kevan, personal observation). The specimen is now housed in the Biodiversity Institute of Ontario at the University of Guelph, and its photograph is accessible on the Barcode of Life Data Systems (Ratnasingham and Hebert 2007): http://www.boldsystems.org/index.php/Public_RecordView?processid=DSCN1024-07.

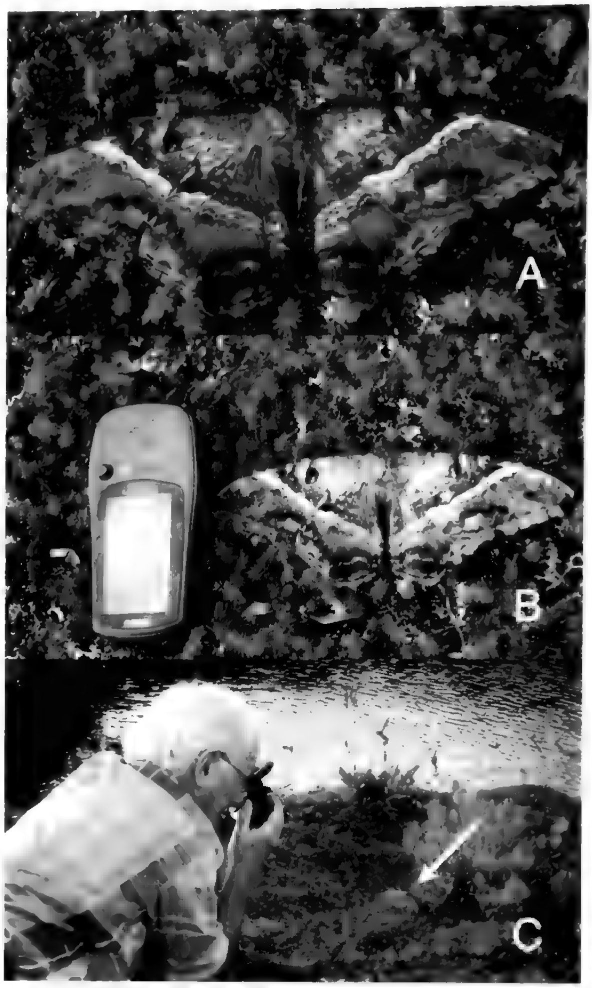

FIGURE 2. The presence of *Ascalapha odorata* (Black Witch) near Churchill, Manitoba. A and B: The worn but living specimen collected near Bird Cove, 18 km east of Churchill, Manitoba, on 18 August 2016. C: Paul Hebert documents the most exciting catch of the day. Photos: T. Ekrem.

Ninety-three sequences from the DNA barcode region of the cytochrome *c* oxidase 1 gene are currently available for *A. odorata* on the Barcode of Life Data Systems (Ratnasingham and Hebert 2007). The records are from a wide geographical range (Figure 1), but all are members of the same Barcode Index Number (cluster) (BOLD:AAA5595*).

The average *p*-distance among these sequences is 0.28%, and the maximum distance is 1.38%. The *p*-distance to the nearest neighbours is 6.6%. Most of the *A. odorata* sequences fall into a single cluster, but the Churchill specimen belongs to a rather divergent group, represented by just three other individuals, two from the Yucatán Peninsula (Mexico) and one from Costa Rica (Figure 3).

Although it may never be possible to firmly establish the point of origin of the Churchill specimen, further analysis of barcode variation in Central and South American populations of *A. odorata* coupled with the

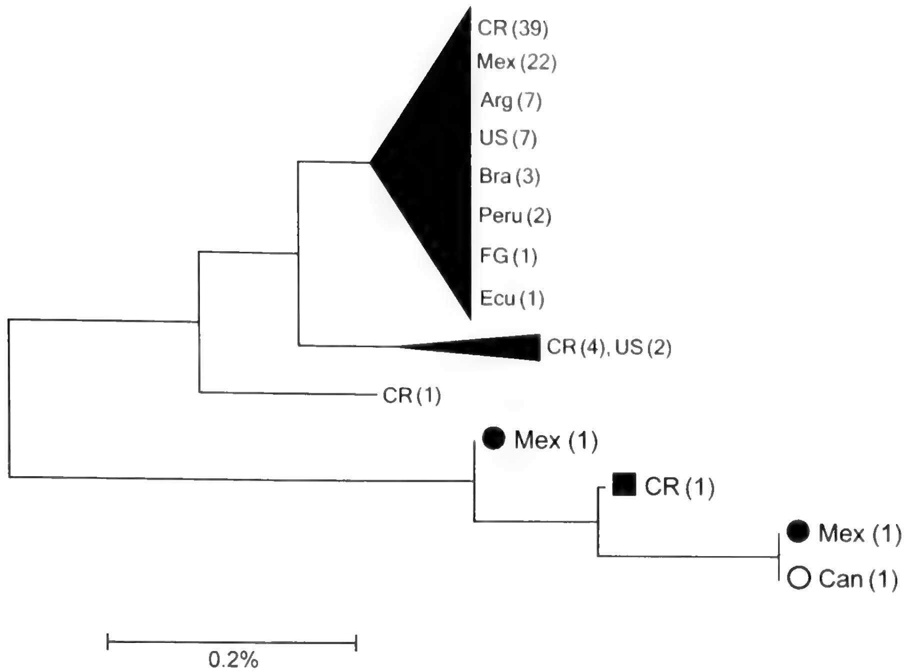

FIGURE 3. Neighbour-joining tree of DNA barcodes for *Ascalapha odorata* (Black Witch). Cluster with the specimen collected near Bird Cove, 18 km east of Churchill, Manitoba, on 18 August 2016, is coded: Churchill (open circle), Yucatán Peninsula (grey dots), Costa Rica (square). The tree was generated using Kimura 2-Parameter distances and pairwise deletion of gaps with MEGA5 (Tamura *et al.* 2011).

analysis of additional gene markers might permit the resolution of this uncertainty.

Acknowledgements

We thank Megan Milton for producing the figure for the neighbour-joining (NJ) tree and Marc Daverdin for producing the distribution map. Fieldwork in Churchill was supported by an International Polar Year grant to PDNH and PGK from the Natural Sciences and Engineering Research Council of Canada (NSERC). Sequence analysis was enabled by a grant from the Government of Canada through Genome Canada and the Ontario Genomics Institute in support of the International Barcode of Life project. We thank Winnie Hallwachs, Cecilia Kopuchian, Daniel Janzen, Carmen Pozo, and Carlos Lopez Vaamonde for allowing the use of barcode records under their curation.

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Received 10 September 2013
Accepted 13 December 2013

Multiple Crossings of a Large Glacial River by Canada Lynx (*Lynx canadensis*)

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Feierabend, Dashiell, and Knut Kielland. 2014. Multiple crossings of a large glacial river by Canada Lynx (*Lynx canadensis*). Canadian Field-Naturalist 128(1): 80–83.

Rivers may act as barriers to the movement of terrestrial mammals, which could limit dispersal and gene flow. Glacial rivers are particularly hazardous because of the cold water temperature and swift current. Yet, we determined that 2 Canada Lynx (*Lynx canadensis*) equipped with GPS collars repeatedly swam across the main channel of the Tanana River in interior Alaska in 2011 as late in the season as November, when the average minimum daily air temperature was −27°C. These observations are consistent with the low level of genetic structure observed in Canada Lynx in northwestern North America and suggest that even large rivers may pose less of a barrier to movement by Canada Lynx than expected.

Key Words: barrier; boreal forests; Canada Lynx; *Lynx canadensis*; dispersal; home range; river; Alaska

Introduction

Rivers may act as barriers to the movement of terrestrial mammals because of the risk of injury or death from drowning (Storm *et al.* 1976; Peres *et al.* 1996; Garroway *et al.* 2011). By limiting dispersal into potentially favorable habitats as well as constraining gene flow, such barriers may have both ecological and genetic consequences (Puth and Wilson 2001). In northern regions, the near-freezing temperatures of glacial rivers add to the dangers posed by swift currents and floating debris.

Whereas large ungulates such as Moose (*Alces americanus*) and Caribou (*Rangifer tarandus*) regularly cross open glacial rivers during seasonal migrations (Griffith *et al.* 2002; Kellie 2005), these rivers presumably pose considerably more danger to medium-sized mammals, such as Coyotes (*Canis latrans*) and Canada Lynx (*Lynx canadensis*).

The only published report of a Canada Lynx crossing an open river describes an individual that swam across a 3.2 km wide section of the Yukon River (Kobalenko 1997). There are several unpublished reports of Canada Lynx crossing open rivers in Alaska and Canada, but the frequency with which individual Canada Lynx make such crossings is unknown. Here, we report the behavior of 2 Canada Lynx that repeatedly crossed the glacially fed Tanana River in interior Alaska during fall and early winter, before the river was sufficiently frozen to allow them to cross on foot.

Methods

Study area

This study took place in the Bonanza Creek Long-Term Ecological Research (LTER) site (65°, −148°) and surrounding areas, approximately 20 km southwest of Fairbanks, Alaska, U.S.A. Upland, lowland, and floodplain boreal habitats in the study area included Black Spruce (*Picea mariana*), White Spruce (*Picea glauca*), Balsam Poplar (*Populus balsamifera*), mixed White Spruce–Alaska Paper Birch (*Betula neoalaskana*), Trembling Aspen (*Populus tremuloides*), and regenerating stands of Alaska Paper Birch, Trembling Aspen, and shrub birch (*Betula* spp.) in areas that had burned in the previous 30 years.

The Tanana River, which is the largest tributary of the Yukon River, flows across the southern edge of the site and is highly braided. The Tanana River has an average discharge volume of 1600 $m^3 \cdot s^{-1}$ with a low of approximately 560 $m^3 \cdot s^{-1}$ in spring and fall prior to freeze-up, but it can reach a maximum of about 2300 $m^3 \cdot s^{-1}$ during floods in late summer (USGS 2013*).

The river is typically frozen from late November until April–May (KK, personal observation). Open-water temperatures in late fall/early winter are just above freezing (KK, unpublished data). Average maximum and minimum air temperatures in the study area were 15°C and 4°C, respectively, in September 2011, 3°C and −6°C, respectively, in October 2011, and −18°C and −27°C, respectively, in November 2011 (Bonanza Creek LTER 2013*).

Canada Lynx capture and collaring

Between June 2008 and November 2012, we used padded Soft-catch® traps (No. 3, Woodstream Corp., Lititz, Penn.), Belisle foot snares (Wildlife Control Supplies, East Granby, Conn.), and home-made cage traps to live-capture 23 Canada Lynx. Scent lures and animal carcasses were used to bait traps. We administered Telazol (3 mg/kg) to trapped individuals using a jab stick, then determined sex and weight, and we fitted 12 individuals with timed-release collars equipped with global positioning system (GPS) loggers, VHF transmitters, and activity sensors (model G2110B, Advanced Telemetry Systems, Isanti, Minn). Collars

weighed 350 g (approximately 2-4% of the mass of Canada Lynx in Alaska) (Alaska Department of Fish and Game 2008*) and were not expected to affect survival (Sikes *et al.* 2011). The activity sensor provided a count of the number of changes in the position of a tilt switch on the collar and represented a unitless measure of an animal's activity. Collars were programmed to record locations at 5-hour intervals.

Capture and handling procedures followed animal care and use guidelines of the American Society of Mammalogists (Sikes *et al.* 2011) and were approved by the University of Alaska Fairbanks Institutional Animal Care and Use Committee (Protocol 135202-3) and the Alaska Department of Fish and Game (Permit 11-041).

Analysis

We report movements for 2 adult Canada Lynx: a male collared from 2 September to 5 November 2011 and a female collared from 15 August to 21 November 2011. We recovered the male's collar after it prematurely released from the animal, and we recovered the female's collar after the animal was trapped by a professional fur trapper. We counted the number of times each Canada Lynx crossed the main channel of the Tanana River as well as major braids and sloughs, based on 0.6-m resolution DOQQ imagery (USDA 2007*) in ArcGIS 10.0 (ESRI, Redlands, Calif.). Crossings were identified by consecutive GPS locations situated on opposite sides of the river. Because Canada Lynx could conceivably have entered and exited the river from the same bank, this count represents the minimum number of times each Canada Lynx was in the river during the sampling period.

We estimated home range sizes using Brownian bridge movement models (Horne *et al.* 2007). Success rates for scheduled GPS fixes were 49% and 61% for the male and female Canada Lynx, respectively. GPS accuracy varied, depending on the orientation of the GPS antenna to the sky and the number and configuration of satellites available.

We estimated location accuracy using two stationary collars programmed to collect fixes at 5-hour intervals in the field under dense vegetative cover and open sky for 60 hours. Using the Standard Distance tool in ArcGIS, we found the standard deviations from the mean centers of GPS locations to be 6.7 m (n = 12) and 3.1 m (n = 12) under cover and open sky, respectively. When calculating Canada Lynx home ranges, we used a conservative estimated location error of 30 m based on data from Horne *et al.* (2007).

We used all GPS location fixes (146 for the male and 287 for the female) over all days fixes were obtained (64 days for the male and 98 days for the female). We calculated utilization distributions using the kernelbb function (adehabitat package) in R (R Core Team 2013*) and extracted isopleths using Geospatial Modeling Environment (Beyer 2012*).

Home range boundaries were defined by 90% isopleths (Börger *et al.* 2006), and core use areas were defined by isopleths (male = 37%; female = 33%) that divided intensively used areas from peripheral areas of less intense use. This was done by fitting an exponential regression to a plot of utilization distribution (UD) area against utilization distribution volume (i.e., isopleth value) and identifying the utilization distribution volume for which the slope of the regression line was equal to 1 (Vander Wal and Rodgers 2012).

We quantified diel activity patterns using average collar activity counts and movement rates derived from distances between consecutive GPS locations. In order to avoid biased movement rates over longer intervals, we used only GPS locations that were 5 hours apart. Because activity accrued and movements occurred over 5-hour periods, we calculated activity and movement for a given time of day as the average of all 5-hour periods containing that time (e.g., activity at 1300 was calculated as an average of activity counts that spanned the time periods 0900–1359, 1000–1459, 1100–1559, 1200–1659, and 1300–1759).

Results

We collected location data from a total of 12 Canada Lynx equipped with GPS collars between December 2009 and January 2013. Of the 10 animals whose data spanned at least one month, 2 Canada Lynx made crossings of the Tanana River when it was frozen in April, 1 male crossed the main channel twice in two days when the river was still open in October, another male crossed the main channel 6 times in November, when the river was likely only partially frozen, and a male and a female repeatedly crossed the unfrozen river between September and November. Only the home ranges of the latter 2 individuals spanned the river.

Of those 2 Canada Lynx, the male made 14 crossings of the main channel of the Tanana River between 4 September and 4 November 2011, and he swam across smaller river braids and sloughs (15-50 m in width) an additional 20 times (Figure 1). The female made 11 crossings of the main river channel between 13 September and 21 November, and she swam across smaller river braids and sloughs an additional 40 times (Figure 1).

We could not determine the exact time of day of most crossings. However, both Canada Lynx crossed river channels multiple times in a given 24-hour period and each animal crossed the main channel at least 3 times at night. The male exhibited a more diurnal pattern of activity than the female (Figure 2). Home ranges were 201 km^2 and 254 km^2 for the male and female, respectively. River water constituted 6% of each home range, and river water constituted 12% and 18% of core use areas for the male and the female, respectively. Both of the Canada Lynx made considerable use of islands in the river (28% of locations for the male and 52% of locations for the female).

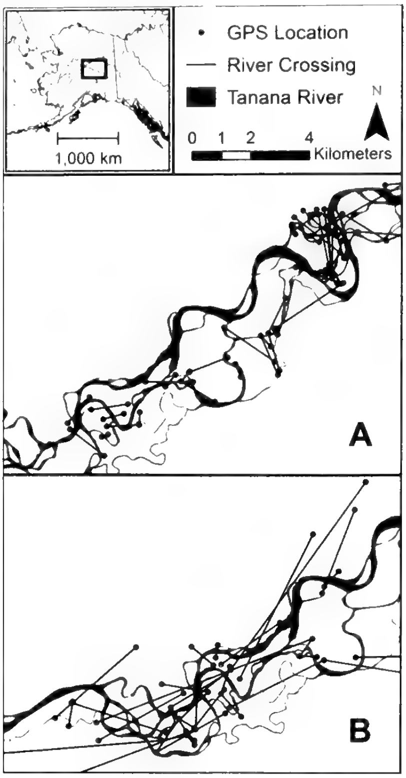

FIGURE 1. Movement across the Tanana River near Fairbanks, Alaska (65°, −148°), by (A) a female Canada Lynx (*Lynx canadensis*) equipped with a GPS collar between 15 August and 21 November 2011 and (B) a male Canada Lynx equipped with a GPS collar between 2 September and 5 November 2011. Lines connect consecutive GPS locations for Canada Lynx on either side of the river but do not indicate the actual routes travelled.

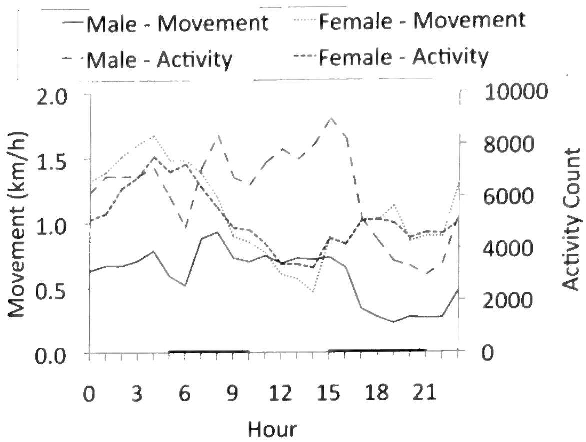

FIGURE 2. Diel activity and movement patterns of a male Canada Lynx (*Lynx canadensis*) equipped with a GPS collar between 2 September and 5 November 2011 and a female Canada Lynx equipped with a GPS collar between 15 August and 21 November 2011 near Fairbanks, Alaska. Activity is quantified as the number of changes in the position of a tilt switch on the collar. Black lines along the x-axis indicate periods of sunrise and sunset.

Discussion

We documented the regular crossing of a large, swift glacial river by 2 Canada Lynx during times of the year when cold air temperatures and initial ice formation elevated the dangers of such behavior. Due to the length of time between GPS locations, we could not determine the exact entry and exit points of the Canada Lynx on the river, but we can be reasonably sure that both Canada Lynx spent considerable time traversing sections of flowing water that were 100–300 m in width.

Assuming an estimated maximum swimming rate of 50 m · min^{-1} (the maximum sprinting speed of a human swimmer is 120 m · min^{-1}) (Toussaint and Trultens 2005) and an actual travel distance twice the width of the river channel (to allow for the current, which was 1–2 m · s^{-1}) (Johnson *et al.* 2010*), we estimate that it would have taken a Canada Lynx 4–12 minutes to cross the main stem of the Tanana River, depending on channel configuration. Moreover, in October and November, shelf ice along the banks of the river could have made exiting the water difficult. Sub-freezing air temperatures surely caused the animals' fur to freeze, drastically reducing its insulative capacity, yet both Canada Lynx often crossed the river multiple times in a single day. We can only speculate as to why these individuals swam across the cold river.

The abundance of Snowshoe Hares (*Lepus americanus*) in the study area reached a cyclical peak in the fall of 2009 and had declined by nearly 50% by the fall of 2010 (Feierabend 2013). We do not have a direct measure of Canada Lynx abundance during this time, but Canada Lynx tracks remained common in the study area through the winter of 2010-2011 despite the declining numbers of "sealed" Canada Lynx pelts (pelts with an official marker or locking seal tag (seal) placed by the Alaska Department of Fish and Game) (all Canada Lynx taken in Alaska must be sealed) in interior Alaska following the winter of 2008-2009 (Alaska Department of Fish and Game 2012*). It may be that Canada Lynx were foraging over increasingly large areas as Snowshoe Hare populations declined. The islands used by the Canada Lynx in this study were up to 4 km^2 in size and could have harbored populations of Snowshoe Hares, but most GPS locations were on much smaller islands that were more likely used as stepping stones during river crossings than for foraging.

Alternatively, the territoriality of neighboring Canada Lynx may have forced the 2 observed individuals to concentrate their movements along the margins of the river. However, given the apparent risks of crossing the Tanana River, one might expect a Canada Lynx simply to cross once in order to explore more suitable habitat in the expansive Tanana Flats to the south. In fact, both individuals did travel up to 30 km southeast of the

river for as long as 12 days at a time before returning to their previous locations, where they again crossed the river.

These observations suggest that even hazardous rivers in freezing conditions may not represent significant barriers to highly mobile mesocarnivores such as Canada Lynx and that foraging movements as well as dispersal that include river crossings may take place under such conditions. This ability to traverse apparent physical barriers is consistent with observations of long-distance dispersal capacity in the Canada Lynx (Mowat *et al.* 2000) and the low level of genetic structure among Canada Lynx populations in northwestern North America (Rueness *et al.* 2003; Row *et al.* 2012).

Acknowledgements

This research was supported by the Bonanza Creek Long-Term Ecological Research program funded jointly by the National Science Foundation (DEB-1026415) and the U.S. Forest Service, U.S. Department of Agriculture (PNW01-JV11261952-231). We thank K. Olson for help in the field and K. Hundertmark, T. Jung, E. Koen, and M. O'Donoghue for critical comments on the manuscript.

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Received 24 October 2013
Accepted 15 November 2013

A Tribute to Kenneth William Stewart, 1936–2011

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Cook, Francis R. 2014. A tribute to Kenneth William Stewart, 1936 2011. Canadian Field-Naturalist 128(1): 84 90.

Kenneth William Stewart, Manitoba herpetologist and ichthyologist, died at Victoria General Hospital in Winnipeg, Manitoba, on 4 July 2011 after an extended battle with the H1N1 virus. Ken was born 30 December 1936 in Madison, Wisconsin, to Drs. John and Gertrude Stewart. Growing up in Clinton, Iowa, he spent much of his youth developing a passion for fishing and nature on the waters of the Mississippi River (Figure 1). He earned a B.Sc. in Dendrology from the Colorado State College of Agriculture and Mechanic Arts (renamed Colorado State University in 1957), Fort Collins, Colorado; an M.Sc. in Marine Biology from the University of Miami, Coral Gables, Florida; and a Ph.D. in Zoology from the University of British Columbia, Vancouver, with a thesis on hybridization between two species of minnow in different genera. Bessie Wenzel (born 1 April 1939) married Ken in Bessie's birth place of Camanche, Iowa, 11 September 1956. Bessie assisted him on many of the field trips during his student years at UBC and was one of the lucky souls to decipher his hand-writing in order to type up his dissertations.

In July 1966, Ken accepted a position in the Department of Zoology at the University of Manitoba as Assistant Professor. From his arrival, he made a major contribution to the remarkable student and staff fellowship of a largely newly recruited zoology department under Harold Welch. Welch had been lured away from the federal Department of Agriculture in the mid-1960s with the challenge of expanding the department, and had quickly blended established researchers like the recently added Casimir Lindsey and veterans like George Lubinsky and Fred Ward, with a bunch of newly minted Ph.D.s from various sources that included, besides Stewart, Mike Aleksiuk, Roger Green, Jack Gee, Roger Evans, and, shortly after, the established W. O. (Bill) Pruitt and others.

"Do ye ken Dr. Stewart at the break of day" (the refrain from a rollicking rendition of an old Scottish melody laced with laudatory original verses depicting Ken's return from all-night frog collecting) still rings heartily in my ears as I write this, decades later. This occasion was an introduction for a departmental seminar presentation by Ken in the winter of 1968–1969 on the developing results of his frog research in Manitoba. This introduction was in partial retaliation for one by Ken for an earlier seminar by Cas Lindsey. Like many endeavours in the zoology department of the University

Figure 1. A young Ken Stewart: beginnings of a lifetime of scientific curiosity at about 1 or 2, probably at Madison, Wisconsin about 1938. Photo: Stewart family album.

of Manitoba at the time, it originated with Lindsey inciting the collaboration of a crew of enthusiastic younger professors and graduate students. This model department generated fresh excitement and productivity virtually daily, a utopia for a student. Not the least in creating this atmosphere of fellowship in the zoology department were the sometimes scathing and always humorous and good-natured barbs contributed by Ken, whose presence ensured that no one lost perspective. Ken was also an enthusiastic participant in (and sometimes victim of) the annual departmental Christmas party skits, where students and professors parodied each other, a tradition brought from the University of British Columbia by Lindsey and his former students.

In 1972, Ken was promoted to Associate Professor and in 1984 to Professor. He retired in 2000 after teaching for 34 years. He gave courses on the biology of fishes, the biology of amphibians and reptiles, the prin-

ciples and process of evolution (jointly with B. J. Hann), the ethics and principles of animal care, and an introduction to chordate zoology. On retirement, he was appointed a Senior Scholar at the University of Manitoba.

Former student Doug Watkinson who co-authored *The Freshwater Fishes of Manitoba*, providing 100 of the 160 photographs commented: "Ken had an amazing memory and was able to cite the Latin names of fishes from all over the world. He was interested in many different fields of science; I know physics was one of his favourite reading topics. I guess another way of putting it is he had a tremendous breadth and depth of knowledge on numerous topics. He loved to teach and was a great story teller. When you were in one of your classes you felt inspired by his passion on the topic. He really seemed to enjoy the people he worked with and the students. He was an avid outdoors person, enjoying fishing and hunting whenever he could find the time. He was keen to share a fishing trip with new University staff and students in his boat on the Red River. If the person did not fish at all that was often all the more reason to take them out. Really he was generous both with his time and sharing his pastime. He had no fear of ethanol, isopropanol or formaldehyde and the possible effects they had on his skin. It was very typical for him to plunge his hands and arms into a vat of fish with 20 year old isopropanol running into his shirt and dripping on his pants. His office was a disorganized disaster to look at but if you asked him for something he would instantly reach into the piles of papers and pull out what he needed. In contrast to his office organization he was meticulous with his notes on whatever project he was working on."

Another former student Gavin Hanke recalls that Ken's lectures on anatomy and lab discussions included tests of attention by mention of the foramen Remington (i.e., bullet holes) in skulls. Gavin also recalled, "Rarely was Ken tricked in return, but it did happen, and he took it with the usual humour we knew to expect. On one occasion he boldly stated that only the extinct acanthodian fishes had pectoral fin spines. Then a student pointed out that his favourite fishing quarry (Channel Catfish) had pectoral fin spines. The look on Ken's face was priceless," as was his response. His early lectures annually featured a guest lecture by Cas Lindsey to present his classic paper on the phylogeny of dragons to demonstrate classification methods.

Ken was an active participant in many zoology department and university committees, developing guidelines as a member (later chair) of animal care and serving on committees at the University of Manitoba and representing it on interuniversity committees throughout his tenure. Included in his other committee contributions was membership and later chair of zoology curriculum review committees.

Ken was also interested in reaching out to the public. He presented lectures and demonstrations related to amphibian and reptile biology at primary and secondary schools, Manitoba Schools Science Symposium, and community organizations, such as Scouts, averaging 12 per year; he made major contributions to conservation in Manitoba by conducting tours of Red-sided Gartersnake (*Thamnophis sirtalis parietalis*) dens in the Interlake district for the Manitoba Naturalists Society (now Nature Manitoba) every year; he was an advisor to the British Broadcasting Corporation on Gartersnake (*Thamnophis sirtalis*) biology during the production of David Attenborough's "Life on Earth" series (approximately 5-minute portion of programme 5) and he was an advisor to film crews from the Canadian Broadcasting Corporation and the Royal Ontario Museum on Gartersnake biology for the production of educational films. He presented interpretive lectures for Manitoba Provincial Parks on Manitoba amphibians and reptiles (Spruce Woods Provincial Park 1981–1991). He served as advisor to the provincial Wildlife Branch on amphibian and reptile biology in 1971–1972 on the status of and protection extended to amphibians and reptiles by revision of the Wildlife Act; in 1972 and subsequently, he provided continuing advice on the regulation of the commercial harvest of Gartersnakes and Northern Leopard Frogs (*Lithobates pipiens*) during a period when biological supply houses were intensively harvesting from the large populations of these species in Manitoba; with the Manitoba Naturalists, he advised on the protection of communal Red-sided Gartersnake dens at Narcisse, where a cluster of dens was designated a Provincial Wildlife Management Area; he advised the Manitoba Conservation Data Centre on the status of fish, amphibian, and reptile species in Manitoba; in 1989 and after, he advised the Wildlife and Fisheries branches regarding control of nesting Double-crested Cormorant (*Phalacrocorax auritus*) populations on Lake Winnipegosis.

During the two years (1968–1970) I spent in Winnipeg, to fulfill the university residence requirement for a Ph.D., and afterward, when I returned to the National Museum of Canada to complete my thesis (among my other duties), Ken doggedly supported my efforts, and the degree was finally obtained in 1978. As a Ph.D. supervisor, Ken was ideal, always generating suggestions for additional approaches and then leaving the student the independence to decide what advice to take and what to use of his own ideas. But he allowed little argument over ruthlessly cutting the verbosity in his students' theses drafts. (If Ken were alive, this tribute would be a fraction of its present length.)

Ken joined field trips with awesome enthusiasm. I recall these with special relish for the successes and comradeship as we investigated the fascinating biological transition zone east of Winnipeg to the Ontario border. Ken and I vied, often separately, in nightly spring outings to plug holes in our understanding of Manitoba amphibian distribution, especially the distribution of call types ("species") of the Gray Treefrog (*Hyla versicolor*). Each morning in the lab, we would

exchange our latest respective successes and individual theories and differing interpretations. He also promoted seldom studied winter herpetology by in-season scuba diving for Mudpuppies (*Necturus maculosus*) in the waters of the Brokenhead River and skidooing on frozen Lake Manitoba to investigate the Leopard Frogs found in the bottom meshes of fisher's nets far out from shore. Jim Johnston took his B.Sc. at the University of Manitoba and was Ken's field assistant until he accepted an offer to be herpetological technician at the National Museum of Natural Sciences in 1972. He stayed until 1979, when his interest in photography led to a position with the Canadian Museum of Science and Technology.

Patrick Gregory arrived in Manitoba a year after I did, after completing his B.Sc. at the University of Toronto. He left with not only a master's degree (1971) but also a doctoral degree (1973), both based on research assisted by the Great Dane Jason on the incredible Red-sided Gartersnake dens in the Interlake area, until then unstudied. It is a tribute to Ken's stimulating role as supervisor that Gregory, Tom Vincent (M.Sc., 1971), and Don Hart (M.Sc., 1975) completed graduate degrees based on snake populations from this area (four theses; eight publications) (Figure 2). Subsequently, Vincent continued his Interlake snake studies in a Ph.D. thesis under Diane Secoy at the University of Regina. Further, Ken interested departmental colleague and physiologist Mike Aleksiuk in the Red-sided Gartersnakes, and Mike with his students added another 14 papers. Then David Crews from Harvard University with Mike Garstska and other students subsequently analyzed the behaviour, pheromones, and other aspects of the Red-sided Gartersnake to extend studies there by over 30 additional papers. Gregory went on to the University of Victoria, where he remains to this day as Professor, with a term served as department head and a succession of papers and students extending the studies of Gartersnake ecology to British Columbia, Alberta, and the Northwest Territories and to other snakes, turtles, and even salamanders and frogs from British Columbia.

Ken did have other graduate students in reptiles and amphibians after Pat and me, so it is untrue that shepherding the two of us to doctorates completely wore out his enthusiasm for herpetology. His change in emphasis was more likely triggered by the departure of ichthyologist Cas Lindsey, who returned to the University of British Columbia. After that, Ken resumed work on his initial interest, fish (even including some palaeontology—a true measure of versatility and flexibility). Former graduate student Gavin Hanke has pointed out that it was fitting that Ken's paleontological interests focused on fishes from the Devonian, the Age of Fishes. A succession of papers and graduate students followed for these lower vertebrates, and Ken extended his field experience occasionally beyond Manitoba with trips to Fiji and Africa.

FIGURE 2. Ken Stewart at a Red-sided Garter Snake (*Thamnophis sirtalis parietalis*) den in the Interlake region, April 1983. Photo: D. Berezanski.

Though brought up farther south and with only an initial introduction to Canada in British Columbia, Ken embraced the shockingly different climate of Manitoba with the same unnerving cheer with which he met any challenge. He added a brace of Malamutes (a breed of Huskies he had come to admire during vacation fishing trips to the Northwest Territories) to his family. These dogs were regularly harnessed to sleds he built himself in the traditional native way. Ken drove them on the streets in his residential Winnipeg suburb and beyond to the surrounding windswept spaces most of us avoided from October until April.

Ken and I shared a commitment to dogs (though we differed greatly on breeds favoured), but Ken drew a personal line on cats. He never could gain acceptance by Tasha, our independent-minded Siamese, who may have realized this, as she invariably quietly welcomed his visits by jumping up on the couch beside him and biting him under the arm. It was a measure of his tolerance that he invariably took this with good humour and restraint, although not without increasing apprehension.

Along with Bessie, he furthered our education beyond herpetology by cooking up batches of fresh-caught local crayfish and catfish (Figure 3) and treating my wife, Joyce, and I to feasts on these. Ken relished both; a taste brought north from his early upbringing in the Mississippi drainage. But I missed out on his sausage-making,

FIGURE 3. Ken Stewart and Channel Catfish (*Ictalurus punctatus*) on the Red River. Photo: Stewart family.

for which Pat Gregory vividly recalls a session : "Ken attached 20 feet (or so) of sheep intestine to a (manual, I think) meat grinder, into which he put his previously prepared mix of sausage meat and seasoning, etc. As the grinder worked away, the sausage mix was forced into the intestine, so Ken had to quickly move to the output end of the machine to twist the lengthening coil here and there to form sausage links. The links were all of different lengths and the whole chain seemed to slowly wind its way around the kitchen like some invading organism."

Cas Lindsey has summed up Ken's contributions: "Ken was a man with a wide range of interests, which he pursued with impressive expertise. Amongst his colleagues and his students he was the accepted source for astonishingly well-informed opinion on almost any topic. He was as versatile in his skills as in his written knowledge; in subtropical seas he was a highly competent scuba diver; in subarctic (Winnipeg) climes he reared husky dogs. He was a mine of information on the academic side of ichthyology, but he was also a skilled and enthusiastic angler. He loved hunting as well as fishing, and he knew a great deal about guns. (He even constructed a firing range in the basement of his Winnipeg home.) Despite his great store of knowledge, he was singularly modest and uncompetitive. Disinterested in self-aggrandizement, Ken preferred teaching to writing. He did not often publish throughout most of his teaching career. But fortunately in 2004 he more than made up for a slow start, and poured a cornucopia of experience into the authoritative and attractive volume *The Freshwater Fishes of Manitoba* (K. W. Stewart and D. A. Watkinson, University of Manitoba Press) (Figure 4). Although this may not be the best way to get NSERC [Natural Sciences and Engineering Research Council of Canada] grants, the book demonstrates there is much to be said for writing your great book *after* you have built up years of experience, rather than the other way around."

Ken and I remained in touch through correspondence and during occasional visits Ken made to Ottawa. I often called on Ken for perceptive and constructive reviews of papers on fish, reptiles, and amphibians when I served as chair of the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) Subcommittee on Amphibians and Reptiles and as editor of *The Canadian Field-Naturalist*.

Ken is survived by his wife, Bessie, of Winnipeg, daughters Kathy (Guy) Plett of Winnipeg and Anne (Rob) Moniuk of Oakville, Ontario, and son John Stewart of Vancouver, British Columbia. Ken also leaves grandchildren Elizabeth (Don Ross) Plett, Guy Plett, Wendy Moniuk, and Victor Moniuk, and great-grandchildren William and Cameron Plett and Alyssa and Ella Ross. A memorial was held in his honour on 8 October 2011 at the University of Manitoba.

FIGURE 4. Ken Stewart (right) and coauthor D. A. Watkinson at the media book launch for *The Freshwater Fishes of Manitoba* in 2004. Photo: University of Manitoba Press.

Acknowledgements

An obituary appeared in the Winnipeg Free Press, 6 July 2011. Appreciation is owed to C. C. Lindsey, Gavin Hanke, Patrick Gregory, Doug Watkinson, and Beverly Horn for their recollections. Darren Gillis, at the University of Manitoba, and Ken's daughters Anne Moniuk and Kathy Plett contributed photographs and further information. D. A. Watkinson advised on contacts and he and Bruce McCulloch provided additional documentation for photographs.

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Received 27 October 2013
Accepted 21 February 2014

Book Reviews

Book Review Editor's Note: We are continuing to use the current currency codes. Thus Canadian dollars are CAD, U.S. dollars are USD, Euros are EUR, China Yuan Remimbi are CNY, Australian dollars are AUD and so on.

Zoology

Into the Night: Tales of Nocturnal Wildlife Expeditions

Edited by Rick A. Adams. 2013. University of Colorado Press, 5589 Arapahoe Avenue, Suite 206C, Boulder, Colorado 80303 USA. 194 pages, 26.95 USD, Cloth.

Except in urban settings, most people avoid the night. But humans are not typical mammals, because most species in this class of animals are nocturnal. However, the eight contributors to this edited book on evening wildlife experiences are not your average person, they are biologists and naturalists fascinated with what goes on when the sun goes down.

The first story recounts the camping adventures of naturalist Stephen Jones in the Sandhill prairies of Nebraska. He studies owls, which has brought him in close encounters with these nocturnal birds. They have visited him in the wild on numerous occasions over the past three decades and have been his personal window on nature. The long-eared owl and its survival has been a particularly poignant species for him and is a harbinger for the progress of civilization.

Dr. Frank Bonaccorso is a wildlife biologist who specializes on studying bats. His story focuses on research in Kruger National Park in South Africa and is interspersed with cat and mouse games of avoiding large mammals such as lions and elephants. He puts little transmitters on fruit bats caught in his nets set near big sycamore fig trees – a keystone species that provides food and shelter for many different animals in an otherwise predominantly open grassland region. It turns out that the only mammal capable of self-powered flight eats a lot of fruits but also is a good disperser of seeds that pass through the digestive tract and are defecated while flying. So I suppose one more thing to watch out for during the night but not a potentially life threatening danger as other things that lurk in the night.

Although not all exclusively nocturnal, the tales of diving in the Galapagos by Christina Allen are certainly dark and mysterious, especially when sharks come into play. But there are two incidents she shares of night time experiences. One is being mesmerized by a mass of bioluminescent marine organisms seen during the first evening on her research vessel that is investigating changes to the island archipelago since Darwin's time. The other is a night dive to find the bizarre and aptly named red-lipped batfish flapping on the ocean floor.

The fourth chapter is written by the editor of the book, Dr. Rick Adams, who is a biology professor at the University of Northern Colorado and a bat researcher. Most of his stories take place in the nearby Rocky Mountains, up to around 4,000 metres in elevation, as he studies the distribution, abundance, and resource use of bats. Some experiences were eerie, such as ghostly images lurking in the shadows, but others were humorous, such as the trailer-eating porcupine that wakes up his field team in the middle of the night.

The next writer takes us to Sulawesi and macaque monkeys, but also reveals her distain for mosquitoes. Dr. Ann Kohlhaas is a professor of biology at California State University in Stanislaus but dreams of her fieldwork in southeast Asia. But it's more than just primates, as she reminisces of wildlife encounters with bats, rats, and snakes. And there are also potentially threatening encounters with earthquakes and malaria.

More tropical adventures are told by Dr. Lee Dyer, a biologist at the University of Nevada in Reno. But these ones take place on the other side of the world in Costa Rica and Ecuador. They are equally as odd with stories of fellow field biologists getting high one night on the local flora and stripping naked before walking into a web of thousands of spiders. Another time after a long night's work, the author gets bit by "a big red and hairy spider" on his private parts and blood is drawn. It ends happily when he wakes up, after stumbling back to his cabin and passing out, to see the stars are still shining.

Not to be left out, a desert encounter with a rattlesnake is told by Dr. James Halfpenny while studying packrats that have been dusted with a fluorescent powder enabling them to be tracked at night to find their middens and hopefully also the beetles they eat that are good indicators of historical changes in climate. But he also tells of snowy adventures as far north as the Arctic, where "nocturnal" work and avoidance of polar bears takes place in the "land of the midnight sun".

The final chapter is left to bat biologist Dr. Scott Pedersen at South Dakota State University in Brookings. He gets to do fieldwork on the Caribbean island of

Montserrat. But it is not all paradise, as he has to deal with erupting volcanoes and pooping bats at night. However, he does survive to give us a recipe for "mountain chicken stew", which is actually a big frog for you foodies out there.

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Owls

By Marianne Taylor. 2012. Cornell University Press (Comstock Publishing Associates), Box 6525, 750 Cascadilla Street, Ithaca, New York 14851-6525 USA. 224 pages, 35.00 USD, Cloth.

In the introduction to *Owls*, British illustrator, photographer, and author Marianne Taylor speculates on the reasons why these birds capture the human imagination so powerfully. She points out that since eye contact is critical to human relations, we are drawn to animals who can return our gaze with two forward-pointing eyes. Most birds, she stresses, have side-mounted eyes for a broader field of vision. She concludes that "owls can truly look at us as we look at them."

The first section of her book, consisting of nine chapters describing owl diversity and natural history, provides insight into how owls see, and explains additional owl senses, attributes and capacities, hunting behaviour and techniques, habitat, breeding biology, conservation issues, and human-owl relations. The second section of the book offers profiles of 41 individual owl species from around the world.

A discussion of the cognitive capacities of owls early in the book adds significant interest. Owl intelligence is apparently little studied, but research has discovered that Barn Owls form extraordinarily detailed auditory maps in their brains, and that the birds have remarkably accurate memories for sounds and their locations. Berndt Heinrich's stories of a hand-reared Great Horned Owl learning to wake him for early meals, gently take food from his hands, and play with inanimate objects for hours provide anecdotal evidence of owl intelligence.

Another intriguing fact, described in a later chapter, further demonstrates owl intelligence, specifically the capacity of the birds to solve problems. Taylor writes about the novel way screech owls deal with flies and other small animals attracted to waste in the birds' nesting cavities. The owls bring live slender blind snakes into the nest to eat the flies, usually leaving the snakes uneaten in return for their services – a fascinating relationship.

Taylor devotes an entire chapter to another relationship, with humans, pointing out that since owls are distributed so widely around the world, most countries have developed distinct owl-related myths and legends. These include owl-like gods and goddesses, owl companions to certain deities, and sundry other links to the supernatural. Some owl symbolism has grown out of the latter connections – for example, early Christian associations of owls with evil, resulting in the unfortunate persecution of owls in related cultures. In other parts of the world, owls – in particular their vocalizations – can be either positive or negative, depending on the type or frequency of the sound

Taylor also writes about owls in literature, television, and film – for example, Winnie-the-Pooh books, Sesame Street, and the Harry Potter series – and about owls in falconry, where they are valued despite (or perhaps because of) the fact that they are known for their reluctance to relinquish prey to their handlers.

The second part of *Owls* starts with a very clear overview of the various owl genera, followed by species profiles describing the bird's range, evolution, relationships, physical features, geographical variation, movements and migration, voice, habitat, behaviour, hunting-diet, and status-conservation.

This part of the book introduced me to unfamiliar owl species such as the Pharaoh Eagle Owl, a large bird of arid and rocky landscapes in north-west Africa, where it typically nests among rocky structures, including the pyramids. I learned that the Collared Owlet of south-east Asia's evergreen forests is the continent's smallest species, but a powerful predator that eats birds up to its own size or even larger – likely the reason it is fiercely mobbed by forest birds when discovered. I was intrigued to read about the fish owls of Asia, who hunt at the water's edge, and whose diet consists mainly of aquatic animals; unfortunately some of these owls are not well known, while the Blakiston's Fish Owl of eastern Russia, China, and Japan (north Hokkaiso Island) is considered endangered.

Owls is a large and beautiful work of photography and writing. Naturalists intrigued by the mysterious lives and uncanny abilities of owls will find the book, with its comprehensive general introduction to the birds, intriguing facts about individual species, and plentiful photographs a worthwhile addition to their libraries.

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A Pocket Guide to Salamanders of Pennsylvania

By Walter E. Meshaka, Jr., and Joseph T. Collins. 2012. The Pennsylvania Heritage Foundation, 225 State Street, Suite 302, Harrisburg, Pennsylvania 17101 USA. 52 pages, 4.71 USD.

This booklet is a companion to *A Pocket Guide to Lizards and Turtles of Pennsylvania* published the same year (reviewed in *The Canadian Field-Naturalist* 126(4): 345-346). It is an identical 15.2 by 9.5 in height and width and only marginally thicker with 12 more pages. The authors are also identical in the two guides but this one is dedicated to Collins, "Whose passion for herpetology was equaled only by his love for sharing it", who had died of a heart attack at 72 before it was printed. The sponsors are the same: The State Museum of Pennsylvania, Pennsylvania Historical & Museum Commission; Wild Resource Conservation Program, Pennsylvania Department of Conservation & Natural Resources; Dickinson College Biology Department; Forgotten Friend Reptile Sanctuary; Friends of Wildwood Lake Nature Center, Inc.; Liberty Environmental, Inc.; Powdermill Nature Reserve; Shippensburg University; and The Center for North American Herpetology.

Like the earlier guide to lizards and turtles, this guide opens with an introduction. This one points out the protected species in the state, officially two endangered, and one threatened. Mentioned as well is the concern expressed by some conservationists over four additional ones. Following this are acknowledgements.

Accounts for the 23 salamander species recorded in Pennsylvania occupy two facing pages for each. On the left are presented the English name, scientific name, total length, and brief highlights on range (in Pennsylvania), habitat, habits, breeding, diet, and conservation considerations. On the right are two illustrations of transformed individuals. For the Eastern Newt both mature adult and immature terrestrial eft stages are depicted. Also on the illustration page is a minute range map with counties in which the species is present in green based on information from the *Pennsylvania Herpetological Atlas* web site and *Amphibians and Reptiles of Pennsylvania and the northeast* by Arthur C. Hulse, C. J. McCoy and Ellen J. Censky. The distributions vary from covering the whole state to barely entering it.

The guide concludes with one photograph of a Spotted Salamander egg mass, another of spermatophores of the same species, and two contrasting the pond larva of the Spotted Salamander with the stream larva of the Spring Salamander, and a checklist of species in the five families represented. A page gives sources of further information on herpetology on websites and publications relevant to Pennsylvania and comments on herpetoculture which stresses current state regulations. The inside back cover has information on the authors and a quote from *At the Planning Commission* by Barbara Meyn in *The Abalone Heart*, 1988: "I forgot to tell them about the salamanders, dark as chocolate, torpid with cold, they move … about this time every year, how easy it is to drive right over them if you are unaware."

Overall, this publication is less than successful for species identification partly due to the darkness of many photographs but primarily because colour and pattern alone are not sufficient to distinguish between some similar forms. Examples are Jeffersonian and Blue-spotted salamanders, and the many dark or red woodland or stream assemblages in Plethodontidae. It should, however, reliably serve for distinguishing the other three Ambystomatidae ([Yellow-] Spotted Salamander, and Marbled [not recorded in Canada] and Tiger [recorded only once in eastern Canada] salamanders), and the single Protidae (Mudpuppy), Salamandridae (Eastern Newt) and Cryptobranchidae (Hellbender) [the latter not occurring in Canada]. Fortunately for use in eastern Canada, 10 of the 15 Pletodontidae do not range this far north. The particularly confusing pairs that do occur in Canada are the plethodontid Northern and Allegany dusky salamanders and the ambystomatid Jeffersonian and Blue-spotted salamanders. A potential source of confusion for Canadian users is that the Red-backed Salamander is represented in the pocket guide only by the red-back phase (red dorsum and gray sides) whereas lead-back (lacking red) and erythristic (all red) phases which might be confused with a southern species, as well as well as other colour variants, occur in Canada with the lead-back reaching 100% in some populations.

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Snapper

By Brian Kimberling. 2013. Pantheon Books, The Knopf Doubleday Group, 1745 Broadway, New York, New York 10019 USA. 224 pages, 28.96 USD, Cloth.

A few months ago, I read a disquieting article in the New York Times on declining bird populations written by Brian Kimberling. While the article was interesting, and well-written, and of course depressing, it also contained a reference to a book by Kimberling entitled Snapper. I was immediately on alert. A book about "my" species? Was I being scooped? Or did this have nothing to do with snapping turtles? I rushed to Amazon, a few keystrokes south, and to my horror, yes it was about snapping turtles, though apparently not en-

tirely. Nevertheless, a few more excited keystrokes and in the next day's mail there arrived a small book with an attractive dust jacket decorated by colourful Audubon-like drawings of birds, which turned out to be Audubon drawings. Not a dust jacket one would associate with snapping turtles. I hurriedly opened the book to scan the Table of Contents. There was none, but there were chapters and Snapper was the title of chapter 2. I settled back in my Lazyboy and started on chapter 1 to build up suspense and prejudice for chapter 2. Thus began a wonderful read of many vignettes by a most accomplished writer and, I surmise, naturalist, on the life and times of a budding biologist/ornithologist named Nathan Lochmueller. Although this is an autobiographical novel, one cannot help feel it is far from entirely fiction. The "snapper" takes up only one chapter and it is obscure to me how the author chose this title for the book. "A Biologist's Adventures among the Rednecks of Southern Indiana" would get more attention and reflect the content better. Even "Ramblings about an Ordinary Youth" or "My Hopeless Love Life while Studying Eagles" might be more attractive to potential readers and still better reflect the story.

Lochmueller is a 20's-year-old biologist, born, raised and sort of maturing in southern Indiana. The book chronicles bits and pieces of his life. Like Bob Dylan's recent "autobiography", Chronicles, this book leaps about with no respect for time and skitters among topics and times without rhyme, reason or warning. To me the writing style, the incorporation of a smattering of interesting natural history, and the description of the lonely, impoverished, slavish life of the underpaid, overworked, dedicated and unappreciated neophyte naturalist makes this a fascinating read. Indeed, I will say without qualm, anyone who is not captivated by the end of chapter 1, is no one I really need to know, and vice versa.

I read the whole book in one short day. I like short books. I liked this one enough that I have since read it more slowly and deliciously twice more. One would like to say it is slightly reminiscent of Stephen Leacock, but sharper, more poignant and critical, edging toward Mark Twain, or even Jon Stewart of the Daily Show. I like his preface quote, "While there is a lower class, I am in it, while there is a criminal element, I am of it, and while there is a soul in prison, I am not free". Or the opening sentence. "I got my job by accident."

The book swerves and slips between amusing yet awed descriptions of Nathan's ornithologist boss, who reminds me of many brilliant biologists I have known and whom I found awesome, and amusing, but never close to. Other memorable characters populate the narrative including, his rogue aunt and uncle from Texas, the Hoosier natives of redneck Indiana, the ivory tower residents of Bloomington, home of Indiana University, and a few feckless friends. But the narrative always returns to Lola, the Maggie May (a la Rod Stewart) love of his life, or at least youth. No male, regardless of his sexual orientation can read this book, and not admit he has known a Lola. Especially if that male was somewhat aimless, and spending six days a week scouring woodlands to map the frail lives of obscure wildlife in the undergrowth. The recent bird researchers in Algonquin Park kept appearing in my picture of young Nathan.

Consider his description of finding the nest of a Kentucky Warbler; "It's like staking out the girl's shower block at summer camp. It can be done, but it takes skill." Oh, hello Hugo.

My problem in reviewing this book is that I want to quote vignettes to reveal the clever humour, the wry regret, the observer's forgiveness, the blatant stabs, the dazzling mix of arrogance and self-deprecation and the pithy commentary on modern humans and our institutions. And the touching and hilarious depiction of a lost opportunity with a woman afflicted badly by Lyme's disease. Nathan attributes to her the description of the Mississippi as "a vast national sow prone to rolling over her young". Nathan then pauses to refer to the ivory-billed woodpecker as Elvis in feathers for both gaudy plumage and regular sightings since declared extinct in 1944. We ecologists all have our Elvis.

Nathan ends his saga of Dana the Lyme's girl by comparing her to his great love, Lola. Lola "belonged to that air conditioned world, Dana understood the squalid and menacing nature of things…the snap of events, Lola's independence was a vain inglorious thing, and my own spotty affair with Lola struck me as trivial, something that dropped out of my sleeve or back pocket, probably not worth picking up." Needless to say, Lola was falling from grace at this point, but she repeatedly reappears, although it is not clear whether it is before or after the above conclusion.

Chapter ix is titled 'Proof'. It describes how Nathan marked a forest of trees by carving Lola's name on all those marked for felling by the US Forest Service plus many others (to temporarily confuse the USFS, a hopeless tactic I confess to using in my youth). I trust that all we Luddite nature lovers have done similarly hopeless things to thwart developers a la Edwin Albee. Nathan then describes a court proceeding utterly reminiscent of my experiences before the Ontario Municipal Board. In this case, a tribunal hears arguments from both sides in a dispute (the cutting or not of trees in a "nature reserve"). This proceeding before a tribunal occurs , "when one side has no prospect of winning". Nathan recounts that the case failed because "it was tried in Indiana, where science, education and Darwin are all equally deplored". The defendants were the US Forest Service whose primary function is "to facilitate timber sales", and the US Fish and Wildlife Service which "truly reveres all woodland creatures provided they can be shot, trapped, hooked, netted or clubbed". At least we know where he stands. Nathan goes on to describe how the lawyers for the defense systematically destroy his credibility and the affidavits of sev-

eral leading ecologist and explains, "a lawsuit is not a work of art, and its aims are to obfuscate what it cannot denigrate until money is free to speak". Such cynicism!

In the end, Nathan comes to some, for me, surprising conclusions, and the fearsome spectre of Darwin rears its ubiquitous embrace. But earlier, our hero thinks back to his days following avian domestic lives, recalling his time, "wandering vast tracts of Indiana woodland and riverbank, taking orders from no one, chronicling the lives, births and deaths and domestic disputes of forest songbirds for biology departments and government agencies. I reveled, like … John James Audubon, two hundred years before me, in the same extraordinary beauty and variety there – reduced every day, by human encroachment, but resilient and resplendent nevertheless". I can't think of a better summary of my own life in the wilds of Ontario and I am sure this echoes the experiences of many readers of the *Canadian-Field Naturalist*. This is a book to be treasured.

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The Crossley ID Guide to Britain and Ireland

By Richard Crossley, and Dominic Couzens. 2013. Princeton University Press, 41 William Street, Princeton, New Jersey, 08540-5237 USA. 304 pages, 27.95 USD, Paper.

I have to admit to a positive bias for Crossley's method of illustration. I know others find the crammed pictures confusing and distracting. But you never see a bird facing right against a plain white background. Well maybe a Shorelark (Horned Lark) on fresh snow is a possibility. Crossley takes computer-manipulated photographs of birds, mounted on to a typical background. This illustration looks like a jigsaw puzzle, with several examples of the species in question dotted throughout the habitat. Most common species have a full page, while the rarer birds have half or a quarter of a page. The author does not follow the current taxonomic order so, for example, all the waterbirds are in sequence. This is a very sensible approach and far more valuable in the field.

My copy arrived a week before I left for England. So I avidly used it to review species I was likely to see. I reminded myself of the difference between Rooks and Carrion Crows. I read through the key points separating Willow and Marsh Tits. I read that Marsh Tit is "One of the worst named birds …" as it prefers deciduous damp woodland – not marshes. The Willow Tit likes scrubby bushes around lakes and that does include willows.

Rather than being put off by the illustrations I found them particularly charming. Swallows (Barn Swallows to us) are shown in a typical farmyard; bright birds against cold, grey stone. There is a quaint flower-filled village as the background for Blackbird and typical churchyard for the iconic (Eurasian) Robin. While the Marsh Tit flits in its woodland but the Bearded Tit is in a marsh.

In Britain I visited Greenwich, Dulwich, Hampton court, Kensington Gardens and Hampton court. I was amazed to realise that after four days I had made several sightings of Rose-ringed Parakeets and yet I had not seen a single House Sparrow. Crossley gives the current estimate of populations where available. For the parakeets he quotes 8,600 pairs, while the sparrows rank at 5.3 million pairs. I eventually saw 20 House Sparrows near Lincoln.

There are other species included that add to the sense of the habitat and give a more rounded idea of the species environment. For example, there is a man raising his arm in defence against Great Skuas. A Badger peeks out from the trees holding Tawny Owls. A Eurasian Red Squirrel, that shares the same limited distribution, adds to the Crested Tit page.

Last week a friend sent a photo of a flock of Common Redshank with their bright coral "shanks" with a slightly smaller yellow-legged bird in the centre. It was one of the over 250 records for Lesser Yellowlegs for the UK. This species does not make it into this book. It covers about 300 out of 596 species on the official British record. Regularly occurring rarities that arrive every year, but in very small numbers are covered, but the more sporadic vagrants are not. As such this guide is more useful to new birders and occasional visitors. Indeed the introduction provides an excellent approach for the new birdwatcher. There are many practical examples of what to do in the field to get the best out of this guide.

So I recommend this book as a first guide for beginners. You can move on to a more comprehensive guide after a couple of year's experience. Visitors will get an introduction to both the birds and the countryside of the British Isles.

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The Warbler Guide

By Tom Stephenson, and Scott Whittle. 2013. Princeton University Press, 41 William Street, Princeton, New Jersey 08540-5237 USA. 514 pages, 29.95, Paper.

Warblers are the crown jewels of the Americas avifauna. Exquisitely plumaged in spring, many assume cryptic plumages in fall, morphing from among the most beautiful of birds to tricky identification challenges. Indeed, for many Canadian observers learning fall warblers is their first great birding milestone. Add to this an array of songs and you have the complete avian package. As an added bonus, warblers are a key part of our summer ecosystem; and witnessing mixed species migration fallout is among the greatest spectacles that await the Canadian birder.

Warblers are well treated in standard field guides, which are more than adequate for most identifications. However, due to their intrinsic beauty and the interest they invoke, several family monographs have been produced, of which this is the most recent. At over 500 pages it is a stay-at-home reference work, not a field guide. It starts with an extensive introductory section including an easy to follow "topographic tour", tips on what to look for, and an extensive segment on how to use sonograms. Indeed, a unique feature of this book is its extensive treatment of vocalizations. Every species has a comprehensive collection of sonograms, and there are stand alone sections visually comparing the songs, chip notes and flight calls of similar species. Not everybody "gets" sonograms, but if you are one of those who does, this will be a selling point. There is also an extensive and well-organized photographic "quick finder guide". Particularly useful for suffers from "warbler neck" are plates portraying undertail patterns. The end pieces include a fun test quiz and an intriguing section on hybrids.

Most of the book consists of species accounts. Every regularly occurring species in North America is exhaustively treated, with multiple photographs of all distinct plumages, close ups of key features, useful studies of comparison species, a treatment of aging and sexing, accurate, easy to read range maps, and sonograms. To provide a random example: the species account for Canada Warbler has 37 photographs, nine sonograms and two range maps (one each for fall and spring migration). Additional photographs and sonograms of the species are found elsewhere in the book. On the other hand, the text is minimalist, consisting mostly of concise descriptions of the key features illustrated in each figure. Rarely occurring species are afforded less space but are more extensively treated than in a standard field guide.

The audience for this book are more experienced observers; neophytes will be better served by standard field guides. The current work will help you figure out if that Common Yellowthroat you are saw was a first winter male or female, sort out American Redstart aging and sexing, or help with that tricky Oporornis identification. I "test drove" the book several times this fall, checking it against birds seen that day or testing to see if it was up to the challenge of identifying "mystery bird" photographs posted to various web groups, which it was, often using second order identification clues beyond those included in standard works.

How does it stack up? The most important comparison is "A Field Guide to Warblers of North America" by Jon Dunn and Kimball Garrett. In effect the two works are complementary, Dunn and Garrett has a more textual approach with detailed written descriptions and greater detail on ecology and range, whereas the current work is unabashedly visual. Warbler officiandos will want to own both. The bottom line? Get this book if you are an experienced observer looking to take your warbling to the next level. Like me, you will probably find yourself turning to it from time to time, either to verify particularly tough identifications or to admire its many fine photographs.

MARK GAWN

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Yellowstone Wildlife: Ecology and Natural History of the Greater Yellowstone Ecosystem

By Paul A. Johnsgard. 2013. University of Colorado Press, 5589 Arapahoe Avenue, Suite 206C, Boulder, Colorado 80303 USA. 248 pages, 31.29 USD, Paper.

Paul Johnsgard is a lifetime naturalist who has published numerous works on taxonomy, natural history, and ecology in the American West especially the Great Plains and the state of Nebraska. His long publication list is filled with natural history monographs of birds of the Rocky Mountains and Great Plains can be found on the University of Nebraska, Lincoln website Digital Commons. His last book on the Wyoming mountain area was published in 1982 entitled *Teton Wildlife: Observations by a Naturalist*, and focussed on different bird species of the area.

The above work, in collaboration with his former student and wildlife photographer Thomas Mangelsen, is a coffee-table sized, soft-cover book of 224 pages with many full and double paged photographs spectacular in their beauty and grand perspective. Landscapes and natural areas as well as birds and mammals in their natural landscapes are featured in Mangelsen's photog-

raphy and many sidebar drawings by Johnsgard himself are included. A quick count rendered 46 photographs and 26 drawings which fill up the book and provide relief in the large pages of text on natural history in the area.

The area featured is the first confusing aspect of the book. The Greater Yellowstone Ecosystem is not only Yellowstone National Park, a name well-known and recognized by tourists and almost all readers, but includes much more regional geography. Chapters are named by their landform areas but only four of the fourteen chapters are located in or near the park and the other ten chapters are located far to the south in regions named Jackson Hole, Grand Teton Park, the National Elk Refuge, and the Bridger Teton National Forest. To the north and east there are Montana and Wyoming cattle ranching areas outside of the parks. A couple of small maps at the beginning of the book locates the chapters in their relative areas but there is no large map to orient the unfamiliar reader with the whole area. The visitor who has had one or two experiences of visiting Yellowstone will quickly realize that these are not areas remembered from driving the ring roads of neither Yellowstone nor day-hiking nearby trails.

The strength of the book is the extensive research which Johnsgard has accumulated on population and conservation data of many of the large mammal species of elk, bison, deer and wolves. Years of population studies on timber wolves as they rose and fell coinciding with the health of the elk population and comments on current herd and wolf pack management are included along with comments on population control decisions. Johnsgard is in favour of annual culls to keep the populations healthy and allowing wolf packs to contribute to the population control. Natural history patterns of other mammals are also included with life history accounts of beaver, bear, bighorn sheep and various smaller mammals. His life history stories of the various animals makes interesting reading for the naturalist who has encountered these species at Yellowstone or in other natural habitats.

The birds of course are Johnsgard's strength and most of his life's work. The book includes many accounts of bird-life written in a story-book fashion following an individual or mating pair forming pairs, nesting-building, and home range defence. Lists of resident birds, mammals, amphibians, reptiles, and fish are all included to complete the vertebrate counts.

I spent many hours reading the text and leafing back and forth through the book to view and revisit the photographs comparing the mammals and birds featured with the appendices giving more research details. It is an attractive book to read in short life-story passages by a masterful story-teller or look at brilliant pictures by an accomplished photographer. As a good story will do, I enjoyed my time with it and thought of more touring in the Yellowstone Plateau region.

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Yellowstone Wildlife: Ecology and Natural History of the Greater Yellowstone Ecosystem

By Paul A. Johnsgard. 2013. University Press of Colorado, 5589 Arapahoe Avenue, Suite 206C, Boulder, Colorado 80303 USA. 248 pages, 31.29 USD, Paper.

The beautiful portrait of a coyote on the cover of *Yellowstone Wildlife* immediately captured my attention since it directly relates to my two books: *Suburban Howls* (on eastern coyotes) and *My Yellowstone Experience*. With my background as a wildlife biologist and an avid traveler to Yellowstone, I was a prime candidate to read this book, which is described in the inset as "a detailed natural history of the wildlife species that call Yellowstone National Park (YNP) and the Greater Yellowstone Ecosystem their home. Illustrated with stunning images by renowned wildlife photographer Thomas Mangelsen, *Yellowstone Wildlife* describes the lives of species in the park, exploring their habitats from the Grand Tetons to Jackson Hole." Herein, I find one of the major confusions of the book: while it initially seems like a book about YNP, in actuality only three of the 14 chapters actually concentrate on Yellowstone with most of the remaining focusing on Grand Teton National Park (GTNP). A slight modification to the title, *Greater Yellowstone Wildlife*, would have more accurately characterized this book which has a more regional approach, as indicated in the "Preface and Acknowledgments" section. There, Johnsgard defines the Greater Yellowstone Ecosystem as 18 million acres of national parks, national forests, national wildlife refuges, Bureau of land Management lands, plus state and private landholdings.

The cover inset additionally summarizes the book, noting "From charismatic megafauna like elk, bison, wolves, bighorn sheep, and grizzly bears, to smaller mammals like bats, pikas, beavers, and otters, to some of the 279 species of birds, Johnsgard describes the behavior of animals throughout the seasons, with sections on what summer and autumn mean to the wildlife of the park. Enhanced by Mangelsen's wildlife photography, *Yellowstone Wildlife* reveals the beauty and complexity of these species' intertwined lives and that of Yellowstone's greater ecosystem." I counted 73 images from cover to cover including 27 illustrations by Johnsgard and 46 photographs by Mangelsen. While these images clearly add to the text, I would have preferred the pictures to have been more closely aligned

with the text along with many additional photos that directly related to the stories (locations and animals) that unfolded in each chapter. Further, the existing images (some being two page spreads) could have been smaller so more could have been squeezed within the existing length of the book. For example, in the discussion of the *Sagebrush Sea* of GTNP, there are two 2-page spreads of coyotes, both from YNP, yet there is not one picture of the scenery from that area of the Tetons.

Each of the 14 chapters focused on specific areas of YNP and GTNP and a natural history story was woven around the lives of notable animals inhabiting those regions, such as: coyotes and pronghorn in sagebrush habitats, gray wolves in Lamar Valley YNP, ravens and other birds (including golden eagles) by the Grand Canyon of the Yellowstone, woodpeckers within recently burned areas, bison around geyser basins, sandhill cranes near willow flats, trumpeter swans and waterfowl in and around ponds, bald eagles and ospreys by oxbows, beavers and elk near aspen stands, grouse and martens in spruce forests, dippers in mountain streams, and picas and bighorn sheep in high elevation areas. The stories in each chapter are very detailed and accurate, for the most part, and Johnsgard has a lengthy section of notes and references at the end of the book to support the behaviours he describes. There were only a few things I questioned, such as the claims that white-tailed deer are bigger than mule deer (I always thought it was the opposite) and male martens help raise the young (I thought that only female Mustelids raised offspring). The notes and references section is impressive with many sources reviewed; the only odd thing was the number of very old literature sources, like a 1934 reference being the main one used for bald eagle natural history, and 1950 and 1959 sources for dippers. However, this did not affect the content of each chapter, so maybe I am being a tad nitpicky here.

Because each chapter was so in depth, I found myself repeatedly trying to find the ultimate meaning of each section other than gaining a glimpse of the daily activities of some of the prominent animal residents in each region. Each chapter usually came to an abrupt end, with a new and unrelated chapter following it, making it difficult for the book to maintain a proper flow. While the descriptions were impressive, there was so much detail in each chapter I felt bogged down with information on landmarks (e.g., streams, rivers, mountain ranges) and animals in each region. A small map of YNP and GTNP at the beginning of the book gave a general location for each chapter, but I believe that each individual chapter needed its own map so the reader could appreciate all of those names and places mentioned and described in detail throughout the book. For instance, I have to admit that I have spent much more time in YNP than GTNP so I found myself getting lost in all of the unfamiliar descriptions of GTNP because I had no diagram to refer to for each section. This was especially evident in Chapter 1, *History of the Greater Yellowstone Ecoregion*, which would more accurately be called *Geologic History of the region* since it is a very heavy read about how the area was created and has changed over millions of years. I found it very difficult to focus on all of the text in that section without seeing some image(s) of the landscape features that "resembles the imprint of a raccoon's right forefoot" (page 2). I was also disappointed that only two paragraphs at the end of that chapter dealt with human use of the area over the past 10,000 years, since there was no other mention of it.

The book has only minor grammatical errors, and most descriptions seem accurate and realistic for the location discussed. The appendices provide necessary information on the wildlife of the region including checklists of mammals, birds, amphibians, reptiles, and even invertebrates such as dragonflies and butterflies. However, and sort of like the majority of the paperback, I felt that a lot of appropriate information was provided but the organization could have been better. For example, birds are mentioned in Appendices 1-3 including a checklist, short descriptions for many birds, and longer descriptions for fewer, more recognizable birds. Thus, the common birds were mentioned in all three appendices. While each list in and of itself was fine, it seems that there could have been a more concise summary of the information presented. Also, while all species were grouped taxonomically to related species, the lists were not made in alphabetical order and it seems that an easier scheme would have aided the reader, like maybe having a sub-column for different groups (e.g., waterfowl, raptors, songbirds). Finally, and to my point above about the need for more coherent structure, some of the appendices include Red Rock Lakes and Grays Lake National Wildlife Refuges, yet I fail to understand the reason for their inclusion since they do not appear in the text up to that point, even if they may technically be located within the Greater Yellowstone Ecoregion (GYE). I had to resort to learning about these refuges by conducting internet searches. I surmise that these places were added because the author compiled all available information on the GYE and included everything even if it was random or repetitive.

Overall, this is a fine natural history book of the GYE and is worthy of putting on your bookshelf, especially for travelers to that region. It provides lots of detailed information on many different resident wildlife species ranging from large mammals to inconspicuous birds, even if a better focus to the book would make it easier and more enjoyable to read. As it appears now, the paperback can certainly be read in sections and used as a reference. I suggest focusing on specific chapters when visiting the GYE to add to your experience of those ecosystems.

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BOTANY

Field Manual of Michigan Flora

By E. G. Voss, and A. A. Reznicek. 2013. The University of Michigan Press, c/o Chicago Distribution Center, 11030 South Langley Avenue, Chicago, Illinois 60628 USA. 990 pages, 25.00 CAD, Cloth.

Many field naturalists in eastern North America will be familiar with Edward Voss's classic, three-volume *Michigan Flora*. But since its publication beginning in 1972, extensive taxonomic changes led many of us to supplement this flora with various updated but often less accessible keys, sometimes photocopied from others, and maybe inconveniently stuffed into a filing cabinet. With the 2012 publication of the *Field Manual of Michigan Flora*, a single pared-down volume offers a reference that compiles the many changes in nomenclature and plant relationships that have occurred in the last four decades. Over 200 new species for Michigan, a large majority of them non-native, have also been described in this new work.

To achieve the synthesis of three volumes into one while including new species, several important changes have been made. Perhaps most notably, the botanical line drawings of selected species have been removed. This turns out to be less of a limitation than I had anticipated, since I have come to rely upon other sources for most illustrations anyway. Distribution maps for Michigan counties are still present but smaller, and thanks to this more compact form, maps are now physically closer to their corresponding species description. Finally, the concise text is now restricted to identification and distribution, with taxonomic debate referenced rather than treated directly. Like others, I have a fondness for Voss' thorough and often witty introductory text to many genera in the original flora, and will continue to refer to it. However, the advantage of this single volume is undeniable.

As with the preceding *Michigan Flora*, the stand-out feature of this work continues to be the clarity and high quality of the keys, which are more accessible to beginners and amateurs than any other volume I know. Couplets consist of precise but clear language, almost always with multiple characters. As before, certain keys even permit identification with only vegetative material (e.g. Potamogetonaceae). Practical identification tips for the field botanist are present in many descriptions. Ontario botanists benefit from native-born co-author Tony Reznicek's extensive knowledge of this area with a number of direct references to Ontario occurrences. The glossary is also substantially more comprehensive, although it would still benefit from a few illustrations for more difficult concepts.

Those already familiar with flora of the area will note many, many nomenclature and taxonomic changes. Some of these follow Flora of North America (FNA) treatments, and some do not. The large number of families and species assignments that have changed since the publication of *Michigan Flora* are helpfully summarized in a three-page appendix (and take note of Liliaceae!). The taxonomic concept is relatively conservative in some difficult and highly variable groups (e.g. *Rubus*, *Amelanchier*), with quite broadly defined species or complexes.

Organizational changes are mostly welcome. The listing of families by alphabetical order (rather than by taxonomic order) makes the manual more accessible to the non-taxonomist. Following this pattern, genera are also given alphabetically within families, and species within genera. For the most part, this makes the book much easier and faster to use.

I have found one significant exception to this, and that is in the organization of the genus *Carex*. In general, the *Cyperaceae* keys are a great strength of these authors, and are among the most-used pages in my copy. However, the alphabetic listing of all *Carex* species descriptions, rather than by section as in the old *Michigan Flora*, does not allow for easy comparison of the descriptions of closely related species (e.g. all Ovales). The location of the key for each species is also not referenced in the index. Since many sections and their constituent species have changed since the publication of *Michigan Flora*, this has left me to flip through over a dozen pages to locate the appropriate section key. The overall result, in my experience, is much less user-friendly than *Michigan Flora*. Fortunately, this shortcoming appears limited to *Carex*, since other large families are sufficiently diverse at the generic level that their keys are more compact.

A minor disappointment relates to the identification of non-native species. Given the large number of new additions of non-native species and the increasing attention paid to them in recent years, I would have liked to see the addition of symbols in each key or description, so they could be obvious at-a-glance. As before, this information is available only in the text of each description.

Still, these issues do not detract greatly from the overall utility of this book. As I expected, this has become my main reference for flora in southern Ontario, which has a species assemblage very similar to Michigan. Weighing in at about 3.5 lbs, the durable hardcover could even fit into a backpack – at least on shorter trips. Thanks to a foundation grant that supported its publication, it is available at an extremely affordable price. Whether you are a recent beginner ready for more information or an experienced field botanist, this practical work is the new standard identification manual for vascular plants not only in Michigan, but in adjacent areas.

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North Pacific Temperate Rainforests: Ecology and Conservation

Edited by Gordon H. Orians, and John W. Schoen. 2013. The University of Washington Press, P.O. Box 50096, Seattle, Washington 98145-5096 USA. 383 pages, 60.00 USD, Cloth.

It's only truly possible to appreciate the geographical complexity of the region covered in this book by flying over it, as I had the opportunity to do this past summer while flying between Seattle, WA, and Fairbanks, AK. There are more than 6000 islands, ranging in size from less than 1 ha to more than 6000 sq km, between the north end of Vancouver Island and Yakutat, near the Alaska-Yukon border. The adjacent mainland is dissected by a handful of large river valleys draining the interior, and numerous small, steep waterways cascading down from the glaciers of the coastal ranges. The biological complexity is correspondingly enormous and of global importance.

The genesis of this book was a science cruise and tightly structured workshop to incorporate conservation biology concepts into management strategies for conserving the biodiversity and ecological integrity of the Tongass National Forest in southeast Alaska, which at 6.8 million ha encompasses 80% of the land area in that region. During the workshop, it was decided to produce a book and to expand the scope to include the broader North Pacific temperate rainforest region. While much of the text still focuses on the Tongass, there is considerable input from the British Columbia part of the rainforest and the concepts are broadly applicable. Each of eight chapters is written by one or more experts in the topic under discussion, which are then synthesised in a final chapter which includes conclusions and recommendations.

Much of the biodiversity and endemism of the region stems from its glacial history when some of the area, particularly along the outer continental shelf, remained ice-free during recent glacial advances (chapter 1). Species colonised the rest of the region from these refugia or along a tidewater route from the north and south, or later along ice-free corridors from the interior of the continent. Preservation of these corridors and linkage sites should be the goal of management plans because gene flow is a critical process with benefits ranging from persistence of small populations to introduction of traits necessary to adapt to fluctuating environments. And fluctuate it will, as the region is expected to experience significant climate change in the future, particularly for the small, steep watersheds where water and nutrients are transported quickly to estuaries (chapter 2). Recent modelling forecasts a shift from hydrological processes dominated by ice and rain-on-snow events to purely rain-dominated responses; discharge will become more seasonal, with lower discharge during summer (the result of fewer glaciers) and higher discharge during winter (more rain than snow). These changes are expected to have regional-scale influences across much of the North Pacific rainforest, and impact estuarine and marine production through effects on amount and timing of carbon and nutrient export. Most riparian management focuses on fish-bearing streams, often ignoring headwater streams, but recent research shows that the structure and function (e.g., inputs of litter, invertebrates and nutrients) of headwaters is important to lower stream reaches. Changes in the life history of invertebrates due to climate change, as well as the magnitude, frequency and duration of floods affecting stream morphology, have huge implications for the adaptation and survival of salmon, a mainstay of wild food webs, aboriginal culture and economic opportunities in the region.

Natural disturbance patterns (chapter 3) are typified by mass wasting events on steep, unstable slopes with thin soils, flooding, avalanches, and many small scale gap disturbances due to wind throw or stem breakage from insects/disease, but rarely from fire. Large-scale clear-cut logging contrasts sharply with this historical pattern of disturbance because of its location on less-steep slopes, larger patches of disturbance, and typical short time to re-harvest. One of the greatest challenges to developing a scientific approach to conservation in these forests is to reconcile the temporal scale and pattern of timber harvesting with the long-term patterns of forest dynamics, complicated by the likely effects of climate change (e.g., it may be drier, so more fires).

Chapter 5 discusses the Tlingit and Haida traditional use of trees, other plants and animals (salmon was especially important), and minerals, and the transition to commercial exploitation. Mining began with the gold rush in the 1880s, followed by silver, copper, lead, zinc, barite and marble, but the early operations were mostly over by the 1940s. High prices for rare earth elements are driving more recent explorations. Large-scale timber harvesting of old-growth forests didn't take off until the 1950s, and are currently uneconomic and require subsidies, while second-growth harvests will likely require even greater subsidies because they are competing with lower-cost products from many other regions around the world.

The short-term economic and social benefits of industrial logging will be paid for by long-term ecological consequences as the result of forest succession and roads – termed succession debt – even though there may be short-term (0-19 years after logging) benefits for some wildlife species, such as deer (chapter 6). Heavy logging reduces winter range (the old growth intercepted snowfall), causing a decline in deer numbers, which humans blame on predators, and the roads allow increased legal and illegal harvest of wolves ... and the cycle continues. It is a perverse irony of the supply system in the US that timber harvesting, with attendant new roads, is necessary for the Forest Service to get funds to decommission, restore and monitor old ones!

Chapters 7 and 8 address the issues of choosing areas for protection in reserves. The concepts of conservation biology are used to discuss three categories of reserve design criteria: reserve content (species, ecosystems and processes internal to a reserve), reserve context (interactions between a reserve and its surroundings, i.e., transboundary processes), and emergent properties (interactions among different components, and between content and context). The authors also raise the question – are intact watersheds good reserves? – and make the determination that they have a better chance of maintaining ecological integrity over the long term without human subsidies, but that smaller size reserves may be beneficial in some cases. Under climate change scenarios, reserves that incorporate a range of climates, site types and elevations will allow for movement within the reserve, and managing the matrix habitat around protected areas to facilitate species migration will be an important component. Conservation strategies that rely on habitat reserves and roadless patches often fail because they ignore the importance and function of the intervening matrix of unprotected lands (e.g., a wolf pack's range is larger than most reserves). Variable retention harvesting (chapter 9), particularly group or aggregated retention rather than dispersed retention, is very important in landscapes that are unlikely to have enough protected areas and reserves to maintain biodiversity on their own. It is important, though, that monitoring of trends and conditions of major indicators (forest structure, windthrow, growth and regeneration, species and biological diversity) be done over an entire landscape, since it is critical to adaptive management practices. However, the authors caution that most adaptive management examples have failed because: 1) lack of funding for monitoring, 2) failure of decision makers to embrace the concept, and 3) lack of leadership to sustain what is a complex, lengthy process.

The final chapter reviews and synthesises the concepts presented, describes lessons learned from years of research, highlights uncertainties and gives suggestions how these might be reduced, evaluates potential new avenues of research, and provides conclusions and recommendations relating to the challenges and promises. Forest managers tend to seek solutions that are a compromise among complementary and competing objectives, which are generally highly technical, scientific solutions to what are truly political problems, and they need to start factoring in global implications, whether or not they are beyond local control. The cornerstone of management or rehabilitation should be to maintain an ability to adjust in the face of changing natural conditions; restoring and maintaining processes that generate habitat, rather than reference conditions, will enable organisms to adapt to change. The authors contend that if managers get the scale of their interventions right, as well as ensuring functional and economic connectivity, they will be well on their way.

Overall, this is a very valuable book which covers the basics of conservation biology and island biogeography theory as applicable to the region, aboriginal and commercial uses of its natural resources, management challenges, and opportunities to find a better way forward. Researchers, students and managers will find it very useful. The centre-piece of 23 black-and-white photographs has excellent captions, some annotated to illustrate concepts or issues with forests. There is a good index and extensive bibliography. Some figures are reproductions from scientific papers, and are small and almost illegible, and having a more legible full-page map of the area would have been helpful.

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OTHER

A Love Affair With the Birds: The Life of Thomas Sadler Roberts

By Sue Leaf. 2013. University of Minnesota Press, Suite 290, 111 Third Avenue South, Minneapolis, Minnesota 55401 USA. 274 + xviii +16 pages, 29.95 USD, Cloth.

Thomas Sadler Roberts was the right man in the right place at the right time. His first passion was birds; in high school in the frontier town of Minneapolis in 1875 he formed, with six other teens, the "Young Naturalists Society." Roberts was the first president; many of their meetings were held in his bedroom, which also served as their library and museum. Only two years after foundation of the Minnesota Academy of Natural Sciences at St. Paul, the lads published original articles on the Black Tern, and compiled a list of 122 species of Minnesota birds and a state list of plants. At their meetings they discussed the works of Elliott Coues and the theory of evolution proposed by Charles Darwin and Alfred Russell Wallace. Roberts was the valedictorian of the class of 11 that graduated from Minneapolis High School in June 1877. He then entered classes at the relatively new University of Minnesota. In his first summer he studied birds at Herman and Lake Minnetonka, publishing the results in the *Journal of the Nuttall Ornithological Club*, the predecessor of *The Auk*. The second summer he took part in a survey of the Lake Superior south shore from Duluth to Grand Marais and began correspondence with key ornithologists George Bird Grinnell, J. A. Allen, William Brewster, and Henry Henshaw. In 1880 he worked as a land surveyor, but watched birds as he surveyed.

From 1882 to 1885, Roberts studied medicine at the University of Philadelphia medical school. His roommate was a young lawyer, Carroll Williams, for whom Roberts's second child was later named. William Osler was one of his clinical teachers, so impressed by Roberts that he visited the Roberts home for breakfast one morning when he was in Minneapolis years later. Roberts then did a residency at the Children's Hospital, Philadelphia, the first pediatric hospital in the United States. There was little time for bird study until he returned to Minneapolis to establish his medical practice in the fall of 1886. He married his friend Jennie Cleveland in October 1887; by March 1892 they had three children.

When he had a patient warranting special expertise in diagnosis or treatment, Roberts would sometimes accompany that patient by train to Rochester, about two hours distant, to consult with his friends, doctors Will and Charlie Mayo. The Mayo brothers later rated Roberts as "one of the five best diagnosticians in the United States." Will Mayo, as a regent of the University, later wrote a letter to University of Minnesota President George Vincent to support the appointment of Roberts to the Minnesota Natural History Survey.

For 25 years, Roberts was a "hard-driving hard-working physician," transported by John Nordquist, living nearby on 24-hour call to drive Roberts' horse and buggy — and later automobile — to home visits. Roberts' nurse would often join in his visits to the summer homes of wealthy industrialists on nearby Lake Minnetonka, often to deliver their babies there. Roberts was the chief of staff at the first Minneapolis hospital, St. Barnabas, from 1893 to 1900. In 1901 he became the unpaid Professor of Pediatrics at the University of Minnesota medical school and then, from 1906, the unpaid Clinical Professor of Children.

Roberts delivered his last baby in 1915, the year the University elected him as the unpaid (for four years!) Professor of Ornithology. He solicited funds from his wealthy friends merely to pay his expenses for specimen collecting trips; a few special families kept him on retainer for medical care. James Ford Bell and John Crosby (heads of the Washburn-Crosby Company that later became multi-national General Mills) were two of his wealthy industrialist friends. Bell himself said: "Roberts has so many friends who have money."

Roberts was an innovator. His first bird photos were exposed onto glass plates at Heron Lake in 1898 with a heavy mahogany camera powered by a small generator. These photographs were acclaimed at the American Ornithologists' Union (AOU) meeting in Washington that year. In the fall of 1916, his second year at the fledgling University museum, Roberts showed Sunday afternoon movies on a projector donated by Bell. That year his first annual ornithology class began with 17 lectures and lab demonstrations followed thereafter by field outings. He helped a bird club organized by the Woman's Club evolve into the Minneapolis Audubon Society. He encouraged Frank and Marie Commons in their unusually intensive bird banding operations on their farm at Lake Minnetonka. The main thrust of the museum in the 1920s was the construction of large dioramas. In February 1926 Roberts began weekly radio broadcasts about Minnesota birds on Washburn-Crosby's new radio station WCCO.

His major obligation was to write the landmark two-volume, heavily subsidized *Birds of Minnesota*, illustrated with colour paintings by Allan Brooks, George M. Sutton, Francis Lee Jacques and Walter A. Weber. It was finally published to great acclaim in June 1932. His beloved wife Jennie died that October. Roberts then resumed making medical house calls to sick patients to earn some money when income-producing bonds defaulted during the worldwide financial crisis.

In 1937, over fifty years after his first visit there with his roommate, Roberts revisited the Williams farm at New Hope Pennsylvania, where Roberts proposed to Carroll's sister Agnes, twice widowed, and she accepted.

In 1938, at his final AOU meeting, held in Washington, Roberts' two-volume *magnum opus* received the prestigious Brewster Medal from the AOU. That year work had finally begun on a new museum building deferred in 1931 when Minnesota, hit hard by the depression, delayed for 9 years its equal match of the large donation offered by James Ford Bell. The elegant Bell Museum of Natural History was not opened until December 1939.

Roberts' stamina persisted well past eighty. In spite of a slight stroke in October 1944, he did not miss giving a single class in ornithology in the spring of 1945. That summer he had another slight stroke. In October Agnes had surgery for hemorrhage and thereafter received long-term care in Franklin Hospital until her death on New Year's Eve. Roberts himself died of a heart attack 19 April 1946 at age 88.

For centuries a disproportionate number of physicians have shown a serious interest in birds. Thomas S. Roberts was one of these. My personal interest in birds was added to my desire to be a physician, when my two aunts in Manitoba joined together to buy me Taverner's *Birds of Canada in 1940*, an expensive book, selling for three dollars, which had seemed too much money for the first aunt to give to a boy only 12 years old. Later my parents bought me the heavily subsidized two-volume *Birds of Minnesota* which also sold for only three dollars per volume; in those two volumes I read about Roberts himself and his medically-trained colleagues P. L. Hatch, Elliottt Coues, E. A. Mearns, and J. C. Hvoslef. These two books and his bird identification key so valuable to bird banders, have held prominent places in my library ever since.

Leaf is too polite to mention the Roberts family finances. Where did Roberts' father, John, gain the financial resources that allowed him to move from a farm in Pennsylvania to reside 25 years in Minneapolis? How

could Thomas and Jennie employ a nurse, a maid, and a chauffeur throughout thirty years of medical practice, and then receive no salary whatever for his first four years at the small initial University Museum?

Sue Leaf has located and reproduced magnificent early and later photographs, from throughout Roberts' life, from 1859 at age 18 months through to 1942. Yet, until he closed his medical office in 1915 after thirty years of medical practice, she makes it clear that, unless he was away from Minneapolis, his patients took precedence over birds. She deserves warm plaudits for her careful scrutiny of a mass of data, both ornithological and medical, that she did not know existed in adjacent cabinets when she did her zoology graduate studies in the same room 35 years earlier.

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Bootstrap Geologist: My Life in Science

By Gene Shinn. 2013. University Press of Florida, 15 NW 15th Street, Gainesville, Florida 32611 USA. xii + 297 pages, 34.95 USD. Cloth.

Much of Gene Shinn's professional life has been spent outdoors in the field. And his life in fieldwork reads as if it has been both highly enjoyable and deeply relished. He has spent his time close to, on, in, and especially under warm sea-water as he investigates carbonate reef systems and nearshore environments. In *Bootstrap Geologist*, Shinn describes his career, the projects and questions that have concerned him, the places he has visited and studied, and the people that he has met and worked with. Why "bootstrap"? Eighty-year-old Shinn positions his autobiography as "the life story of a successful self-taught geological scientist, initially handicapped by lack of advanced degrees, who rose to the top of his profession and received its highest award", the Twenhofel Medal of the Society for Sedimentary Geology in 2009. Throughout his account, he emphasizes the practical aspects of fieldwork, describing the many different types of apparatus he has helped to design and build, from underwater coring devices to samplers and lo-tech monitoring equipment. This is the career of a skilled and intuitive "hands-on" technical specialist, an expert at spotting a problem, and devising a means and an apparatus to investigate it.

Following college studies in zoology, Shinn's early career, between 1958 and 1974, was in the oil industry, when he worked for Shell, first in Florida and Texas, then in Qatar and the Persian Gulf, then in Louisiana and Texas again. In 1974, he moved to work for the United States Geological Survey (USGS), where he continued his offshore research, notably as the director of a specialized marine research work group based in Florida. Here, his practical skills were put to good use in keeping the group operational and busy, despite budgetary and other challenges. Retiring from the USGS in 2006, Shinn's career has continued through association with the University of South Florida. So he has seen the research world from three quite different perspectives: as an employee of a large multinational company, as a government servant working for a major federal agency, and as an affiliate with a mid-sized university. His account shows how, despite working under diverse administrative and funding regimes, he has always managed to follow and maintain his research interests in marine carbonate ecosystems, through tailoring his projects to the circumstances of his employment and taking advantage of opportunities to apply his skills as they present themselves, including such odd applications as exploring hydrogen bomb craters off Pacific atolls.

Taking the mantra of "the present is the key to the past" seriously, Shinn has focused his research efforts on investigating modern carbonate systems, especially subtropical offshore reefs and tidal flats, in the waters around Florida and the Gulf of Mexico, in the Caribbean, off the Philippines, and in the Persian Gulf. Born as a "salt-water conch" on Key West, he spent his late teenage years as much in sea-water as by it, becoming an accomplished spear-fisher and starting a long acquaintanceship with coral reefs. A major thread running through his work has been the way in which marine organisms build up reefs and other biogenic structures and the factors that influence the growth and lithification of reefs. His work is situated at the interface between biological and geological systems, and is therefore notable for the light that it sheds on both. The initial motives for undertaking this modern analogue research were pragmatic, springing from the need to better understand ancient carbonate rocks and especially reef systems because of their role as host rocks for hydrocarbon deposits. He has used the insights gained from work on modern reefs to interpret ancient reefs and carbonate rocks, for example, by coring algal reef mounds in New Mexico. Other applications include the documentation of modern stromatolites off the Bahamas, the recognition of hurricane and storm-derived mud layers in tidal channels near the Bahamas, the elucidation of sabkha stratigraphy in Qatar, and the identification of algal mud production in Florida Bay.

The results from several of Shinn's investigations have challenged conventional views. He describes studies in which his team concluded that "drill mud had not affected the growth of corals" near the Philippines, discovered that "if there was an abundance of junk at the site, there was more fish" when investigating old drill sites off the west coast of Florida, and found "little lasting harm" from offshore drilling near the Florida

Keys. He also studied the movement of groundwater through the carbonate bedrock underlying southern Florida, an issue that has significant implications for assessment of anthropogenic impacts on the environment and the long-term viability of drinking water supplies. This work started in the late 1980s with an investigation of shallow groundwater near a garbage dump in south Florida. He discovered that "pollutants were restricted to freshwater in a highly porous zone above a regional impermeable layer just seventeen feet below the [ground] surface". In other words, the landfill containment leaked. His later studies in the 1990s, funded in part due to concerns over water levels in the Everglades, showed that pollutants and sewage from expanding developments on the Keys were moving through the highly porous limestone and into sea-waters around the offshore reefs. His team conducted dye-injection experiments to show that the flow of the shallow groundwater beneath the Keys is towards the Atlantic, a phenomenon he attributes partly to "tidal pumping". However, despite a network of monitoring wells, Shinn and his team were unable to "prove that sewage contaminated groundwater was killing the reefs" due to enhanced algal growth stimulated by nutrient influxes from sewage.

In recent years, Shinn has considered other reasons for reef die-offs. Noting a correlation between die-offs since the mid-1980s and increased input of African dust, he is convinced that, at least in the Florida and Caribbean reefs, this is more than coincidence. Shinn's research associates have analyzed incoming dust showing that it carries, besides fine-grained clastic material, various biotic materials including bacteria and spores, some of them potential pathogens. Yet dust has been a factor in these ecosystems for millennia; Charles Darwin noted dust fall in mid-Atlantic in 1832 during the second *Beagle* voyage and reported on its organic content (Darwin 1846, *Geological Society Journal* 2: 267-274). What is not clear to me from Shinn's discussion here is why the dust should have become more deadly for reefs in recent decades.

The results of Shinn's studies have not always been well received. Conclusions from his dust research are controversial. As he remarks for the Florida Keys drill sites study, his team "didn't find and document the widespread death and destruction that was expected" nor did they "find what the public, the media, and the academic community wanted". Though he has followed the evidence where it led, he does paint himself as a bit of a contrarian. Shinn expresses little interest or confidence in modelling or theory, highlighting that his work has been "very field oriented". He also has a jaundiced view of permits and regulations that he sees as strangling the capacity to do research, especially in national parks or protected areas. His memoir is fascinating for highlighting changes in research methods between the late 1950s and now. Some of the methodological quandaries we grapple with today were simply not considered decades ago. For example, Shinn writes about using dynamite to create "explosures", holes in coral reefs, in the early 1960s when "few cared about the environmental effects of dynamite". It is difficult to imagine explosives as an approved research tool for reefs now! Perhaps not all changes in the research milieu are bad.

Shinn's writing style is laboured in places and sprinkled with superfluous exclamation marks, but it becomes more readable as the book goes on. There are early digressions into tangential matters that would have been better omitted; the distasteful story of a deeply disturbed physician being one. Shinn's narrative is more assured and interesting when he is writing about his professional career. I was intrigued by his descriptions of ex-pat life in Doha, Qatar, for example. I enjoyed his stories about various field exploits, including a recurrent fascination with "whitings", lime mud precipitated from sea-water that forms white cloudy patches in the ocean. Only in recent years has the role of planktic cyanobacteria in these precipitates been recognized. Exciting new research suggests that such ancient mud may be implicated in the origin of some Middle Eastern oil deposits. Shinn hopes this "hypothesis survives the test of time and future investigation". Certainly, his field observations and substantial research contributions will remain valuable. And anyone interested in modern and ancient reef systems will find much to captivate them in Shinn's entertaining memoir of his industrious and energetic life in sunshine and sea-water.

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Tracks and Shadows: Field Biology as Art

By Harry W. Greene. 2013. University of California Press, 2120 Berkeley Way, Berkeley, California 94704-1012 USA. xiii + 280 pages, 29.95 USD, Cloth.

Harry Greene, a professor at Cornell University, is the author of the classic herpetology book *Snakes: The Evolution of Mystery in Nature*. His new book is part memoir, part profile of the great herpetologist Henry Fitch, and part meditation on snakes and the quest to understand them.

In many ways this is a tale of two herpetologists: Fitch and Greene. Henry Fitch was born in 1909 and although educated in a one-room school-house he went on to become a professor at the University of Kansas. Before arriving in Kansas, he was drafted into the army during World War II, serving as a medic in Europe.

After the war, Fitch eventually landed a job with the University of Kansas in 1948. A dedicated field biologist, Fitch published nearly 200 scientific papers and although he is mainly known as a herpetologist he also published papers on plants, snails, spiders, mammals and birds. His most amazing contribution is a 50-year study of the snakes of the Natural History Reservation owned by the University of Kansas (and now re-named the Fitch Natural History Reservation in his honour). He continued conducting field work into his 90s. When queried by Greene about his favourite animals, Fitch replied "Alligator lizards, copperheads, and garter snakes, because of their interesting natural histories" (page 228).

Harry Greene's father was in the US air force and the family moved repeatedly. Before Greene finished high school he had lived in five different states. He had an early and profound interest in nature, particularly snakes. At age 12, having met herpetologist Charles Carpenter, Greene announced to his parents that someday he too would be a professor of herpetology. His first publication, a brief note on the vestigial defensive display of a species of blind cave salamander, was published when he was just 16 years old. After graduation from high school he got to spend the summer working with Henry Fitch. To help pay his way through university, Greene got a job as an ambulance worker, dealing with car crashes, heart attacks and more than his share of death. Greene was drafted into the army during the Vietnam War and, like Fitch, served as a medic. Greene fully expected to be sent to Vietnam, but ended up being stationed in Germany, where he spent nearly two years before returning to civilian life and graduate school back in the USA. Fascinated by snake behaviour, Greene examined behavioural ecology from an evolutionary point of view, first in coral snakes for his master's thesis and then in constrictors for his PhD.

While part one of the book explores the background of Fitch and Greene, part two, focuses more on snake biology, ecology and evolutionary history. Greene has managed to turn his research on snakes into a global pursuit resulting in stories about Terciopelos in the rainforests of Costa Rica, Green Anacondas in Brazil, Green Bush Vipers in Uganda, and a 15 year study of Black-tailed Rattlesnakes in Arizona. Along the way Greene muses about the co-evolution of primates and snakes. The first snakes evolved over one hundred million years ago. It doesn't seem unreasonable that the early constrictors preyed upon early primates, possibly shaping their evolution and contributing to people's fear and fascination with snakes.

There are many books filled with empty facts about animals and there are also many about people's personal experience with nature, but lacking intellectual depth. Greene's book offers fascinating insights into snake biology and evolutionary history from a true expert, but also portrays the human side of exploring nature, conducting science and struggling through life. This fusion would not work without Greene's evocative writing that captures both the richness of biological life and the fragility of our own lives. This is not just a book for snake lovers, but for anyone enthralled by nature and life itself.

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Alfred Russel Wallace (2013) *On the Organic Law of Change: A Facsimile Edition and Annotated Transcription of Alfred Russel Wallace's Species Notebook of 1855–1859*

Annotated by James T. Costa. 2013. Harvard University Press, 79 Garden Street, Cambridge, Massachusetts 02138 USA. xii + 573 pages, 49.95 USD, Cloth.

Let me say it right up front: I love this book! Reading it is a bit like listening in on the musings of an eminent colleague, trying to follow their train of thought, catching bits of their reasoning and ideas, and being impressed by their knowledge and insights. Tracing the development of Wallace's thinking on biogeography and evolution as shown through this notebook is both a challenge and a pleasure. Watching him tussle with concepts, such as the definition of a species or the distinction between variety and species, is fascinating. These are concepts that biologists and palaeontologists still struggle with and discuss. Reading about his energetic collecting activities is also absorbing, even though his accounts of orangutan hunts are harrowing. As with any colleague, you don't always agree with everything they do. On the other hand, his strenuous and uncomfortable travels and efforts to conserve and ship his collections elicit wry smiles of empathy.

Wallace is an endearing character. He started life disadvantaged by social circumstances and poverty but by dint of intelligence and incredible hard work turned himself into an outstanding naturalist and scientific thinker. Costa describes him "as the greatest biogeographer of his century." The story of how he came up with the idea of natural selection while recovering from fever in a hut on a remote island is well-known. In a rather touching display of trust, he sent his resulting essay "*On The Tendency of Varieties to Depart Indefinitely from the Original Type*" to Charles Darwin, who received it in June 1858 and was devastated to realize that someone else had had the same idea as him. In a hastily-organized presentation facilitated by Charles Lyell and Joseph Hooker, Wallace's essay and a summary of Darwin's thoughts were read together at a meeting of the Linnaean Society in London on July 1, 1858. Darwin, who was on the spot and had the better

PR machine, has always had the lion's share of the glory for coming up with the idea of natural selection. Yet, to his enormous credit, Wallace seems never to have harboured a grudge or expressed any resentment toward Darwin. He seems to have had a rare modesty and generosity of spirit.

Wallace lived for 31 years longer than Darwin, dying in 1913 at the age of 90. In later life, his reputation became somewhat diminished, in part because of his interest in topics such as spiritualism. His scientific stature was not widely recognized during the 20th century, nor was the range of his achievements well known. He was mainly remembered for defining Wallace's Line. This important biogeographic division between the fauna and flora of the Asian and Australian regions was another discovery that arose from his work in the Malay Archipelago recorded in this notebook. However, in recent years, Wallace has been receiving more recognition for his independent discovery of natural selection and evolution. Perhaps this is because the Darwin bicentennial in 2009 stimulated much in-depth re-examination and re-evaluation of the history of thought concerning evolution in the 19th century. Perhaps it is because with the clarity of hindsight and temporal distance we can now evaluate the contributions of both men more dispassionately. As Costa comments in his introduction, today both "are equally honoured as pioneers and discoverers of one of the most profound insights into nature – and ourselves – yet grasped by humanity."

This facsimile edition Wallace's important notebook has been released in time to commemorate the centenary of his death and as a celebration of his life. It showcases one of ten surviving notebooks generated during his travels in the Malay Archipelago between 1854 and 1862, one of the most formative and influential intervals in his life. The other notebooks comprise field notes, specimen records, and journals. This Species Notebook, started some months after his arrival in Singapore in April 1854, includes accounts of his fieldwork and collecting. But it is more than that. In the interstices between his field activities, Wallace read deeply, especially Lyell's *Principles of Geology*, and recorded his thoughts about what he was reading in this notebook. For Wallace as for Darwin, Lyell seems to have acted as a catalyst for thought; indeed, this incitement to thought was arguably Lyell's most important contribution to science. Wallace was especially concerned to document the points where he disagreed with Lyell – and there were a lot of them – and work out his own counter-arguments. These arguments could have formed the basis for his own book on evolution, a book he never wrote, although, as Costa sadly remarks, it is "the book that should have been." From the perspective of his thinking on natural selection, Wallace's lengthy musings on the fossil and rock records and their implications and the nature and relationship of plant parts are particularly interesting.

The breadth of Wallace's interests and observations is impressive. He described his search for birds of paradise and comments on their varying morphologies and behaviours. He considered and developed a "Plan to stop the further increase of Synonyms," the underlining perhaps emphasizing his frustration with the state of taxonomy, by proposing that a central authority should decide on precedence of names and adjudicate disputes over synonyms. As Costa points out, this anticipated the establishment of the International Commission of Zoological Nomenclature by several decades. Wallace identified and collected many species of insects, primarily beetles and butterflies, especially large and showy taxa, and this notebook contains many observations of their behaviour and habitat preferences, as well as some delightful and detailed drawings.

Wallace also expended much thought on the distinction between instinct and learned behaviour, especially as regards the construction of birds' nests. There are many pages of notes and commentary on this topic in this notebook. It was this train of thought, moreover, that eventually led him to consider the problem of human cognition. In 1869, after returning from his travels in the Malay islands, Costa recounts that Wallace "publicly declared that the human brain could not be explained by natural selection, and that therefore human consciousness and cognitive abilities must be the product of a divine plan of some kind." Unsurprisingly, this viewpoint led to a split with Darwin, and probably in part accounts for his diminished reputation in later years.

Although it spans the interval when he wrote his famous essay, the Species Notebook contains no comments, drafts, or obvious notes related to that work. Readers will share Costa's frustration at the "maddeningly little information" from Wallace during "the very period in which he had his insight into natural selection and penned the landmark paper." His notes do record his bouts of illness and the many "hot rain night[s]" he endured. Perhaps this is explanation enough for his rather perfunctory record of his stay on Ternate and the neighbouring island of Gilolo, now called Halmahera, the place where he actually wrote his essay. "If only," laments Costa, "Wallace had jotted something about his momentous breakthrough." Well, he didn't, but the notes he did leave us make for fascinating if demanding reading nonetheless.

This book is beautifully designed and laid out. The left-hand page has a facsimile of a page from Wallace's notebook, with the handwritten text transcribed next to it. Some facsimile pages include Wallace's drawings or even, in a few cases, pasted in specimens. It is remarkable how clear Wallace's handwriting is, whether he is working out the proper dimensions for specimen labels, writing an account of a day in the field, or tallying his collections. There are few scribbled, illegible, perfunctory or blotched notes here. The facing right-hand page has annotations compiled by Costa, includ-

ing additional information about the life-forms, people, places, and incidents mentioned in Wallace's notes. These are sometimes accompanied by illustrations from Wallace's later publications or other near contemporary sources. Costa also provides background contextual information about Wallace's ruminations on species questions and what he has been reading. These annotations are insightful, informative, and often lengthy. They add greatly to the value of this book and, indeed, many of Wallace's notes would not be comprehensible without these extensive and knowledgeable comments. Costa has done a tremendous job of ferreting out and elaborating the sometimes opaque references in the notes, especially the mention of people who were probably well known at the time but are now obscured by history. In presenting the Species Notebook to us, Costa has produced a work of admirable scholarship. This book will certainly help to elevate Wallace to his rightful place in the pantheon of 19th century natural scientists and garner him additional respect as an original and perceptive thinker.

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NEW TITLES

Prepared by Roy John

† Available for review * Assigned
Currency Codes – CAD Canadian Dollars, USD U.S. Dollars, EUR Euros, AUD Australian Dollars.

ZOOLOGY

* **Amphibians of Ohio.** Edited by Ralph A. Pfingsten, Jeffrey G. Davis, Timothy O. Matson, Greg Lipps, Jr., Doug Wynn, and Brian J. Armitage. 2013. Ohio Biological Survey, P.O. Box 21370, Columbus, OH, USA, 43221-0370. 916 pages, 90.00 USD, Cloth.

Animal Earth. By Ross Piper. 2013. Thames & Hudson, 181A High Holborn, London, UK, WC1V 7QX. 320 pages, 45.00 USD, Cloth.

Animals of the Serengeti and Ngorongoro Conservation Area. By Adam Scott Kennedy, and Vicki Kennedy. 2014. Princeton University Press, 41 William Street, Princeton, NJ, USA, 08540-5237. 152 pages, 27.95 USD, Paper.

A Field Guide to the Ants of New England. By Aaron M. Ellison, Elizabeth J. Farnsworth, and Nicholas J. Gotelli. 2012. Yale University Press, P.O. Box 209040, New Haven, CT, USA, 06520-9040. 416 pages, 33.46 CAD, Paper.

Phillipps' Field Guide to the Birds of Borneo, Sabah, Sarawak, Brunei, and Kalimantan (Third Edition, Fully Revised). By Quentin Phillipps, and Karen Phillipps. 2014. Princeton University Press, 41 William Street, Princeton, NJ, USA, 08540-5237. 384 pages, 35.00 USD, Paper.

Birds of Kenya's Rift Valley. By Adam Scott Kennedy. 2014. Princeton University Press, 41 William Street, Princeton, NJ, USA, 08540-5237. 264 pages, 29.95 USD, Paper.

Birds of the Serengeti and Ngorongoro Conservation Area. By Adam Scott Kennedy. 2014. Princeton University Press, 41 William Street, Princeton, NJ, USA, 08540-5237. 224 pages, 27.95 USD, Paper.

Ten Thousand Birds. By Tim Birkhead, Jo Wimpenny, and Bob Montgomerie, 2014. Princeton University Press, 41 William Street, Princeton, NJ, USA, 08540-5237. 544 pages, 45.00 USD, Cloth.

Beetles of Eastern North America. By Arthur V. Evans. 2014. Princeton University Press, 41 William Street, Princeton, NJ, USA, 08540-5237. 544 pages, 35.00 USD, Paper.

Bumble Bees of North America – An Identification Guide. By Paul H. Williams, Robbin W. Thorp, Leif L. Richardson, and Sheila R. Colla. 2014. Princeton University Press, 41 William Street, Princeton, NJ, USA, 08540-5237. 208 pages, 24.95 USD, Paper.

The Fauna of British India Including Ceylon and Burma – Butterflies Vol. 1. By G. Talbot. 2013. Today & Tomorrows Printers and Publishers Karol Bagh, Delhi, India, 110005. xxx + 600 pages, 1000.00 INR (about 18.00 CAD).

Wildlife of the Caribbean. By Herbert A. Raffaele, and James W. Wiley. 2014. Princeton University Press, 41 William Street, Princeton, NJ, USA, 08540-5237. 304 pages, 19.95 USD, Paper.

Conus of the Southeastern United States and Caribbean. By Alan J. Kohn. 2014. Princeton University Press, 41 William Street, Princeton, NJ, USA, 08540-5237. 528 pages, 99.50 USD, Cloth.

* **Deer.** By John Fletcher. 2014. The University of Chicago Press, 1427 East 60th Street, Chicago, IL, USA, 60637. 207 pages, 16.02 USD, Paper.

† **Dolphin.** By Alan Rauch. 2014. The University of Chicago Press, 1427 East 60th Street, Chicago, IL, USA, 60637. 207 pages, 16.02 USD, Paper.

Britain's Dragonflies – A Field Guide to the Damselflies and Dragonflies of Britain and Ireland – Third Edition. By Dave Smallshire, and Andy Swash. 2014. Princeton University Press, 41 William Street, Princeton, NJ, USA, 08540-5237. 208 pages, 25.95 USD, Paper.

Lost Animals – Extinction and the Photographic Record. By Errol Fuller. 2013. Princeton University Press, 41 William Street, Princeton, NJ, USA, 08540-5237. 240 pages, 29.95 USD, Cloth.

The Amazing World of Flyingfish. By Steve N. G. Howell. 2014. Princeton University Press, 41 William Street, Princeton, NJ, USA, 08540-5237. 48 pages, 12.95 USD, Cloth.

Life on the Rocks: A Portrait of the American Mountain Goat. By Bruce L. Smith. 2012. University of Colorado Press, University Press of Colorado, 5589 Arapahoe Ave., Suite 206C, Boulder, CO, USA, 80303. 192 pages, 34.95 USD, Cloth.

A Field Guide to the Larger Mammals of Tanzania. By Charles Foley, Lara Foley, Alex Lobora, Daniela De Luca, Maurus Msuha, Tim R. B. Davenport, and Sarah Durant. 2014. Princeton University Press, 41 William Street, Princeton, NJ, USA, 08540-5237. 320 pages, 29.95 USD, Paper.

* **Octopus.** By R. Schweid. 2014. The University of Chicago Press, 1427 East 60th Street, Chicago, IL, USA, 60637. 207 pages, 16.02 USD, Paper.

Introduction to Marine Plankton. By Abhijit Mitra, Kakoli Banerjee, and Avijit Gangopadhyay. Daya Publishing House, A Unit of Astral International Pvt Ltd., 81, Darya Ganj, Near Hindi Park, Delhi Medical Association Road, New Delhi, India, 110002. 102 pages, 12.00 USD.

* **Rabbit.** By V. Dickenson. 2014. The University of Chicago Press, 1427 East 60th Street, Chicago, IL, USA, 60637. 207 pages, 16.02 USD, Paper.

The Extreme Life of the Sea. By Stephen R. Palumbi, and Anthony R. Palumbi. 2014. Princeton University Press, 41 William Street, Princeton, NJ, USA, 08540-5237. 256 pages, 27.95 USD, Cloth.

* **How Snakes Work: Structure, Function and Behaviour of the World's Snakes.** By Harvey Lillywhite. 2014. Oxford University Press, 198 Madison Avenue, New York, NY, USA, 10016. 24 pages, 54.05 CAD, Cloth.

A Sparrowhawk's Lament – How British Breeding Birds of Prey Are Faring. By David Cobham, and Bruce Pearson. 2014. Princeton University Press, 41 William Street, Princeton, NJ, USA, 08540-5237. 256 pages, 35.00 USD, Cloth.

BOTANY

* **Braiding Sweetgrass: Indigenous Wisdom, Scientific Knowledge, and the Teachings of Plants.** By Robin Wall Kimmerer. 2013. Milkweed Editions, 1635 West 12th Avenue, Vancouver, Canada, V6J 2E3. 320 pages, 24.00 CAD.

Trees of Western North America. By Richard Spellenberg, Christopher J. Earle, and Gil Nelson 2014. Princeton University Press, 41 William Street, Princeton, NJ, USA, 08540-5237. 448 pages, 29.95 USD, Paper, 60.00 USD, Cloth.

Trees of Eastern North America. By Gil Nelson, Christopher J. Earle, and Richard Spellenberg. 2014. Princeton University Press, 41 William Street, Princeton, NJ, USA, 08540-5237. 656 pages, 29.95 USD, Paper, 65.00 USD, Cloth.

OTHER

* **Tracks and Shadows: Field Biology as Art.** By W. Harry. 2013. University of California Press, 1445 Lower Ferry Road, Ewing, NJ, USA, 08618. 296 pages, 29.95 USD, Cloth.

* **A Love Affair with Birds: The Life of Thomas Sadler Roberts.** By Sue Leaf. 2013. University of Minnesota Press, Suite 290 111 Third Avenue South, Minneapolis, MN, USA, 55401. 29.95 USD.

* **The dismal state of the Great Lakes.** By James Pinson Ludwig, 2013. Xlibris LLC, 1663 Liberty Drive, Suite 200, Bloomington, IN, USA, 47403. 273 pages, 20.95 USD.

Marine Community Ecology and Conservation. By Mark D. Bertness, John F. Bruno, Brian R. Silliman, and John J. Stachowiczi. 2013. Sinauer Associates, Inc., 23 Plumtree Road, P.O. Box 407, Sunderland, MA, USA, 01375-0407. 675 pages, 109.95 USD, Cloth.

* **On the Organic Law of Change — A Facsimile Edition and Annotated Transcription of Alfred Russel Wallace's Species Notebook of 1855–1859.** By Alfred Russel Wallace. (Introduction and notes by James T. Costa). 2013. Harvard University Press, 79 Garden Street, Cambridge, MA, USA, 02138. 592 pages, 49.95 USD, Cloth.

News and Comment

Upcoming Meetings

Meeting of the Canadian Botanical Association 2014

The 50th annual meeting of the Canadian Botanical Association hosted by the IRBV, an institute for research in plant biology, the Montreal Botanical Garden, Space for life, and the Université de Montréal to be held 15–18 June 2014 at the Montreal Botanical Garden, Montreal, Quebec. The theme of the meeting, "50 years of Botany in Canada", will focus on the important contribution of Canadian researchers to the development of plant biology. More information is available at http://www.irbv.umontreal.ca/cba-meeting?lang=en.

International Conference on Biodiversity & Sustainable Energy Development 2014

The 3rd International Conference on Biodiversity & Sustainable Energy Development to be held 24–26 June 2014 at the Valencia Conference Centre, Valencia, Spain. The theme of the meeting is: Milestones of innovative scientific research in biodiversity and its allied areas. Registration is currently open. More information is available at http://www.omicsgroup.com/biodiversity-sustainable-energy-conference-2014/index.php.

Botany 2014 Meeting

The annual Botany conference to be held 26–30 July 2014 at the Boise Center in Boise, ID. This annual meeting is a multiple scientific society conference (American Bryological and Lichenological Society; American Society of Plant Taxonomists; Botanical Society of America; American Fern Society; International Association of Plant Taxonomists) serving over 6000 plant scientists whose research and practice span the globe. Registration is currently open. More information is available at http://www.botanyconference.org/.

Book Reviews

News and Comment

Mailing date of the previous issue 127(4): 14 January 2014

THE CANADIAN FIELD-NATURALIST Volume 128, Number 1 2014

Articles

Notes

Tributes

(continued on inside back cover)

ISSN 0008-3550

The CANADIAN FIELD-NATURALIST

Published by THE OTTAWA FIELD-NATURALISTS' CLUB, Ottawa, Canada

Volume 128, Number 2 April–June 2014

The Canadian Field-Naturalist

The *Canadian Field-Naturalist* is published quarterly by The Ottawa Field-Naturalists' Club. Opinions and ideas expressed in this journal do not necessarily reflect those of The Ottawa Field-Naturalists' Club or any other agency.

Website: www.canadianfieldnaturalist.ca/index.php/cfn

All manuscripts intended for publication except Book Reviews should be addressed to the Editor and sent by e-mail: editor@canadianfieldnaturalist.ca **or postal mail (with disk):** 611 Chemin Cregheur, Luskville, QC J0X 2G0; (819) 455-1087; **Book-review correspondence should be sent to the Book Review Editor by e-mail:** r.john@rogers.ca **or postal mail:** 2193 Emard Crescent, Ottawa, ON, K1J 6K5

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Subscription rates for individuals are $40 (online only), $50 (print only), or $60 (print + online). Libraries and other institutions may subscribe for $60 (online only or print only) or $90 (print + online). All foreign print subscribers and members (including USA) must add $10 to cover postage. The Ottawa Field-Naturalists' Club annual membership fee of $40 (individual), $45 (family), or $20 (student) includes an online subscription to *The Canadian Field-Naturalist*. Members can receive printed issues of CFN for an additional $30 per volume (four issues). For further details, including discounts for members of the Canadian Museum of Nature, see http://ofnc.ca/member.php. The club's regional journal, *Trail & Landscape*, covers the Ottawa District and regional Club events and field trips. It is mailed to Ottawa area members, and is available to those outside Ottawa on request. It is available to libraries at $33 per year. Subscriptions, applications for membership, notices of changes of address, and undeliverable copies should be sent to subscriptions@canadianfieldnaturalist.ca or mailed to: The Ottawa Field-Naturalists' Club, P.O. Box 35069, Westgate P.O., Ottawa, ON, K1Z 1A2 Canada. Canada Post Publications Mail Agreement number 40012317. Return postage guaranteed.

COVER: A female and male Ferruginous Hawk (*Buteo regalis*) standing on the rim of a nest containing their young 30 km SE of Hanna, Alberta, June 1990. Photo: Janet Foster. See article by Schmutz *et al.* on 145–150 in this issue.

The Canadian Field-Naturalist

Volume 128, Number 2 April–June 2014

Effectiveness of Stream Sampling Methods in Capturing Non-native Rusty Crayfish (*Orconectes rusticus*) in Ontario

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Reid, Scott M., and Jane Devlin. 2014. Effectiveness of stream sampling methods in capturing non-native Rusty Crayfish (*Orconectes rusticus*) in Ontario. Canadian Field-Naturalist 128(2): 111–118.

Habitat alteration and species introductions have contributed to the decline of native crayfish in Ontario. Although lake populations of crayfish in Ontario are monitored, there is no corresponding program for streams. We used removal-based sampling to evaluate the efficacy of three sampling techniques (backpack electrofishing, hand capture, and seining) to characterize native and non-native crayfish populations in six streams in the Kawartha Lakes region and five streams in the Muskoka/Haliburton Lakes region. All types were effective at detecting non-native Rusty Crayfish (*Orconectes rusticus*). Rusty Crayfish were collected from 65% of samples, constituted 90% of the total catch, and were the only species present in 30% of streams. Compared with other methods, electrofishing was more likely to capture additional crayfish species. Removal-based sampling was not a reliable approach for estimating capture probability and population size. Failure of the removal model was due to increases in the number of crayfish captured after the first pass or too few individuals collected. Mean capture probabilities for electrofishing (0.30) and hand capture (0.31) did not result in reliable population estimates. Compared with seining, electrofishing and hand capture resulted in more sexually active males (fewer sexually inactive males) and more small (< 25 mm carapace length) individuals. For each method, there were differences in capture probability among length classes. A combination of electrofishing and seining (with multiple passes) would maximize species detection, permit sampling of a range of habitat types, and be easily integrated into existing stream fish surveys.

Key Words: invasive species; monitoring; Rusty Crayfish; capture success; streams; *Orconectes rusticus*; Ontario; electrofishing; hand capture; seining; Appalachian Brook Crayfish; *Cambarus bartonii*; Calico Crayfish; *Orconectes immunis*; Allegheny Crayfish; *Orconectes obscurus*; Northern Clearwater Crayfish; *Orconectes propinquus*; Virile Crayfish; *Orconectes virilis*

Introduction

Almost half of the freshwater crayfish species in North America are considered imperilled, making crayfish second only to freshwater mussels in terms of conservation concern (Butler *et al.* 2003; Taylor *et al.* 2007). Worldwide, habitat alteration and non-native crayfish are considered to be the key threats to native crayfish species (Taylor *et al.* 2007). In Ontario, urbanization, draining of wetlands, and acid rain have had a negative effect on crayfish habitat (Guiasu 2007, 2009; Edwards *et al.* 2009). Also contributing to the decline of native crayfish in Ontario is the spread of Smallmouth Bass (*Micropterus dolomieu*) and the non-native Rusty Crayfish (*Orconectes rusticus*) (Edwards *et al.* 2009; Phillips *et al.* 2009).

The Rusty Crayfish has moved or been transported (via bait buckets) into Canadian waters from the northern limits of its natural range in the Ohio River basin of the United States (Rosenburg *et al.* 2010*). In other parts of the Laurentian Great Lakes basin, the major methods of Rusty Crayfish introduction include the release from bait buckets by recreational anglers, the intentional release by aquarium hobbyists, and their introduction by lake users to control nuisance weeds (Olden *et al.* 2011). Where introduced, the Rusty Crayfish has caused dramatic changes to aquatic ecosystems including the replacement of native crayfish, damage to macrophyte beds, and shifts in macroinvertebrate and fish assemblages (Phillips *et al.* 2009).

The Rusty Crayfish was first reported in Canada during the 1960s in Lake of the Woods in northwestern Ontario and a small number of south-central Ontario lakes (Crocker and Barr 1968). It has subsequently been captured in numerous lakes and rivers in other regions of the province (Berrill 1978; Momot 1996; Edwards *et al.* 2009). Although trends in the status of native and non-native crayfish have been monitored across hundreds of south-central Ontario lakes (Edwards *et al.* 2009; Somers and Reid 2010*), a corresponding program has not been developed for Ontario streams and rivers. Given the labour-intensive nature of removing the Rusty Crayfish, a highly fecund species, the like-

lihood of successful eradication or control is largely dependent on early detection (Hamr 2010; Lieb *et al.* 2011a). However, the absence of a standardized, coordinated monitoring program prevents a defensible assessment of the status of native crayfish and the impact of Rusty Crayfish (and another non-native species, Allegheny Crayfish, *O. obscurus*) in flowing waters and limits opportunities for timely remedial action at newly invaded locations.

Selection of sampling method is an important part of the design of monitoring programs. In this study, we assessed the effectiveness of three methods of stream sampling (backpack electrofishing, hand capture, and seining) in capturing Rusty Crayfish. These methods were selected because of their past use to survey stream crayfish assemblages (Jezerinac 1991; Guiasu *et al.* 1996; Sibley and Nöel 2002; Heath *et al.* 2010), their current use to monitor stream fish in Ontario (Stanfield 2005*; Portt *et al.* 2008*), and their suitability for sampling in habitats where wading is possible. Baited traps are often used to sample crayfish in Ontario (Guiasu *et al.* 1996; Somers and Reid 2010*). However, traps were not evaluated in this study as they require repeat site visits, are vulnerable to vandalism or theft (Bernardo *et al.* 2011), and their deployment may be impractical in shallow or fast-flowing water.

A removal-based sampling strategy (depletion) was used to assess the effectiveness of each method in capturing and characterizing the abundance of native crayfish and Rusty Crayfish and differences in probability of capture related to size and reproductive form. Removal-based strategies have been used successfully to assess the efficiency of techniques for sampling stream-dwelling crayfish (Rabeni *et al.* 1997; Alonzo 2001) and fish (Amiro 1990; Reid *et al.* 2009). Unlike mark-recapture methods, they also do not require multiple sampling visits.

Study Area

The study was undertaken along six streams in the Kawartha Lakes region (44°18'N, 78°19'W) — Fleetwood, Jackson, Jennings, Meade, Riverview, and Thompson creeks — and five streams in the Muskoka/Haliburton Lakes region (45°9'N, 79°4'W) — Dickie Lake outlet and Blairhampton, Cinder, Coca-Cola, and Moot Lake creeks.

Sampling locations — ten sites in the Kawartha region and five in the Muskoka/Haliburton region — were selected using recent Rusty Crayfish collection records (EDDMapSOntario 2014*). They represent a range of water temperatures (mean 16.2°C, range 6°–25°), conductivity (mean 353 µs/cm, range 8–990 µs/cm), channel width (mean 5.3 m, range 1–13.6 m), and streambed materials. Seven of the ten crayfish species reported to occur in Ontario are found in these regions. Of those not found, two (Devil Crayfish, *Cambarus diogenes*, and Digger Crayfish, *Fallicambarus fodiens*) are obligate burrowers (Crocker and Barr 1968); thus, the effectiveness of sampling methods for these species must be tested separately (e.g., Ridge *et al.* 2008).

Methods

Fifteen removal-based samples were acquired for each sampling method. Electrofishing and hand-capture were undertaken along reaches of riffle and shallow-run habitat. For these two methods, unit sampling distance was set at 20 m. Seining was undertaken in deeper-run and pool habitats, where this method is more suitable. A 10-m unit sampling distance was set for seining. This shorter distance was chosen because of the limited size of pool and deeper-run habitats in these streams and the typical extent of habitat sampled with a seine during stream fish inventories (Bonar *et al.* 2009). The mean area of stream sampled was: electrofishing 110 m^2 (range 31–228 m^2); hand capture 79 m^2 (range 22–211 m^2); and seining 65 m^2 (range 24–112 m^2). The dominant material in streambeds at sites where seining was carried out was typically finer (clay and sand) than at electrofishing and hand-capture sites (gravel, cobble, and bedrock). Sampling occurred between 29 July and 19 October 2010 and was completed before Rusty Crayfish initiated burrowing activity associated with winter hibernation (Hamr 2010).

At each unit, the sampling area was isolated with 3.2-mm mesh block nets. Electrofishing was undertaken with a Smith-Root Type 12A backpack electrofisher (pulsed DC settings: 300–400 V, 50–60 Hz, 4–6 ms; Smith-Root Inc., Vancouver, B.C.); one or two people, depending on channel width, used nets to pick up crayfish; and sampling rate was 10 s/m^2. Hand capture involved two or three people moving upstream, overturning rocks, and collecting crayfish by hand or using an aquarium net (Hamr 2007*). Seining was carried out by two or three people pulling a bag seine (3.2-mm mesh bag with 4.8-mm mesh wings) upstream. A minimum of three passes were made for each sampling unit. At each unit, effort was standardized among sampling passes. Additional sampling passes were made if a decline in crayfish catch (i.e., depletion) was not observed. Overall, the mean number of passes for each sampling method was similar (electrofishing 4.0; hand capture 4.1; and seine 4.3).

Crayfish captured at each pass were held in separate bins until processed. Individual crayfish were identified to species (Crocker and Barr 1968) and reproductive form: female, male form I (sexually active), and male form II (sexually inactive). For all crayfish, carapace length (CL) was measured to the nearest 0.1 mm and injuries (e.g., missing chelae) were noted. Batch weight of each species was measured to the nearest 0.01 g for each pass. Photographs were taken and voucher specimens were preserved in 70% ethanol for later confirmation of field identification. Voucher specimens were not retained after species identification was confirmed.

Data analysis

Population size (number of individuals) and capture probability were estimated for all crayfish species captured as well as for Rusty Crayfish using multiple-pass data and the maximum weighted likelihood method (Carle and Strub 1978). Catches of individual native species were low and inconsistent and, therefore, not suitable for analysis. The efficiency of sampling equipment is affected by crayfish size and sex (Alonzo 2001; Ogle and Kret 2008); therefore, estimates of capture probability were derived for each reproductive form of Rusty Crayfish and for four classes of CL (≤ 10 mm, 11–20 mm, 21–30 mm, and > 30 mm). Although small mature individuals have been reported, Rusty Crayfish with CL less than 20 mm are generally considered immature (Hamr and Berrill 1985; Hamr 2010). Multiple-pass data were analyzed with Removal Sampling (version 2) software (Seaby and Henderson 2007*). The constant probability of capture assumption was tested using a χ^2-based statistic (Seber 1982). Using the DeLury method (Ricker 1958*), capture probability was also estimated from the total biomass of all species of crayfish collected and the biomass of Rusty Crayfish.

Sampling events were assessed based on whether a decline in catch was observed with successive passes (i.e., depletion); capture probability; and e%, a measure of the precision of population estimates (calculated as 95% confidence interval*100/N) (Penczak and Romero 1990). Penczak and Romero (1990) proposed the following four-point scale to assess e%: 1, very good estimates (< 10%); 2, good estimates (11–25%); 3, adequate estimates (26–50%); and 4, poor estimates (> 51%).

As seining was used in a different habitat type, statistical comparisons among methods were limited to electrofishing and hand capture. Between-method differences in frequency of depletion were tested using Fisher's exact test (Sokal and Rohlf 1995). Differences in capture probability and the representation of each sex (proportion of Rusty Crayfish males in each sample; Alonzo 2001) were tested with the unpaired t-test. Percentage data were arc-transformed before analysis. Graphic inspection of length frequency distributions and the Kolmogorov-Smirnov (K-S) test (based on separate pooled datasets for all crayfish species and for Rusty Crayfish) were used to assess differences in the size of crayfish captured (Zar 1984; Dorn *et al.* 2005).

Results

Six species of crayfish were collected from stream sites: Appalachian Brook Crayfish, *Cambarus bartonii* (n = 131); Calico Crayfish, *O. immunis* (n = 2); Allegheny Crayfish (n = 1); Northern Clearwater Crayfish, *O. propinquus* (n = 32); Rusty Crayfish (n = 2082); and Virile Crayfish, *O. virilis* (n = 1). The Rusty Crayfish was collected from 65% of sampling units, comprised 90% of all crayfish captured and 85% of the crayfish biomass, and was the only species collected from four of the 11 streams sampled (Table 1). It was found in all Kawartha Lakes region streams except for Fleetwood Creek, where only a single Allegheny Crayfish was captured. Despite its presence in nearby lakes, the Rusty Crayfish was not collected from any Muskoka/Haliburton Lakes region streams. Only native crayfish species (Appalachian Brook Crayfish, Northern Clearwater Crayfish, and Virile Crayfish) were collected from these streams.

For all sampling methods, the Rusty Crayfish was typically collected during the first sampling pass (> 88% of sites where present). Overall, electrofishing resulted in the capture of all six species, whereas Calico Crayfish and Allegheny Crayfish were absent from both hand-capture and seining samples. The Appalachian Brook Crayfish was not collected during seining, and capture of the Northern Clearwater Crayfish and the Virile Crayfish required multiple hauls.

Seining was the least time-intensive method, requiring on average 1.2 min/m^2 for sampling and processing. Hand capture was the most time intensive at 3.9 min/m^2, while electrofishing required 2.6 min/m^2.

Population size

Electrofishing always resulted in crayfish capture. In contrast, no crayfish were collected at three hand-capture sites and five seining sites. For 53% of samples, we were able to estimate total crayfish population (all species) and capture probability. In most other cas-

TABLE 1. Comparison of catch data for Rusty Crayfish, *Orconectes rusticus*, using three sampling methods in 11 Ontario creeks.

Variable	Electrofishing	Hand capture	Seining
No. sites yielding Rusty Crayfish	10	9	7
Total number captured	918	1091	73
Females (%)	458 (49.9)	548 (50.2)	35 (48.0)
Form I males* (%)	174 (19.0)	158 (14.5)	22 (30.1)
Form II males* (%)	258 (28.1)	380 (34.8)	16 (21.9)
Total biomass (g)	2739	2555	332
Mean carapace length (mm [SE])			
Females	19.6 (0.30)	17.6 (0.24)	24.7 (1.16)
Form I males	23.0 (0.37)	24.3 (0.32)	25.8 (1.05)
Form II males	17.3 (0.27)	16.0 (0.19)	16.6 (1.15)

*Form I male = sexually active, form II male = sexually inactive.

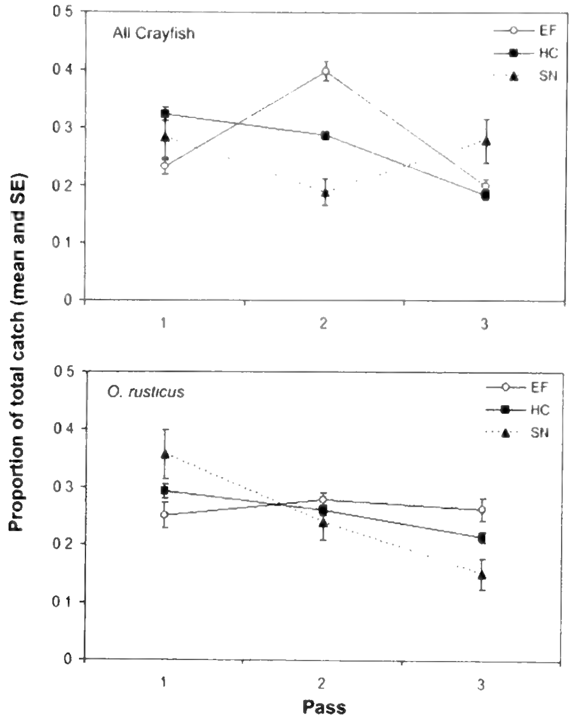

FIGURE 1. Proportion of total catch of crayfish of all species (above) and Rusty Crayfish, *Orconectes rusticus* (below) captured during the first three passes using three removal-based sampling methods in 11 Ontario creeks: electrofishing (EF), hand capture (HC), and seining (SN). Symbols indicate mean values and vertical lines represent standard errors of the mean.

es, either too few individuals were captured (42% of failed estimates), or there was no decline in catch with successive passes (46% of failed estimates) (Figure 1). There was no significant difference in the percentage of samples in which depletion occurred with successive passes between electrofishing (60%) and hand capture (66%) (exact test, $P = 1.0$). Depletion occurred less frequently (33%) in seined samples.

Estimates of total crayfish population were highest for hand-captured samples and lowest for seining (Table 2). In contrast, mean capture probability was highest for seining (Table 2). There were no significant differences in capture probability between electrofishing and hand capture ($t = 0.23$, $P = 0.82$). All estimates resulted in capture probability > 0.2, and, therefore, are considered valid (White *et al.* 1982*). However, capture probabilities for electrofishing and hand capture were below the level considered to provide consistently reliable results (≥ 0.4, Seber 1982). Based on e%, most electrofishing (83%) and hand-capture (86%) estimates were considered at least adequate; 60% of seining estimates were poor.

For 63% of sampling events at Rusty Crayfish sites, we were able to estimate population size and probability of capture. There was no significant difference in the frequency of depletion between electrofishing (60%) and hand-capture samples (70%) ($P = 0.63$), and the frequency of depletion (60%) was similar at seining sites. Differences among methods and estimates of population size and capture probability were similar for Rusty Crayfish and all crayfish species (Table 2). There were no significant differences in capture probability between electrofishing and hand capture ($t = -0.57$, $P = 0.58$). Based on e%, most estimates based on electrofishing (78%), hand capture (80%), and seining (60%) were considered at least adequate.

Biomass estimates were less suitable for comparing sampling methods than abundance data. For both Rusty Crayfish and all species, only 30% of sampling events permitted estimates of population size and capture probability based on biomass. However, capture probabilities for electrofishing and hand capture were similar to those derived from abundance estimates (Table 2).

Reproductive form

For Rusty Crayfish in all samples, the sex ratio was close to 1:1. Males captured by electrofishing and hand capture were more often form II, whereas seining resulted in the capture of more form I males (Table 1). There was little difference in the overall proportion of females captured by the three methods. No significant difference was detected in the proportion of males collected by electrofishing and hand capture ($t = 0.06$, $P = 0.95$).

For 40% of samples, we were able to estimate capture probability by reproductive form (Table 3). For

TABLE 2. Estimates of population size, in terms of abundance and biomass, and capture probabilities for all crayfish species and for Rusty Crayfish, *Orconectes rusticus*, based on three sampling methods used in 11 Ontario creeks: electrofishing (EF), hand capture (HC), and seining (SN).

	Population estimate (mean [SE])			Capture probability (mean [SE])		
	EF	HC	SN	EF	HC	SN
Abundance (no./m^2)						
All crayfish species	1.04 (0.31)	2.48 (1.12)	0.11 (0.05)	0.30 (0.04)	0.31 (0.04)	0.56 (0.13)
Rusty Crayfish	1.30 (0.41)	4.20 (1.80)	0.11 (0.04)	0.29 (0.03)	0.26 (0.04)	0.47 (0.05)
Biomass (g/m^2)						
All crayfish species	5.08 (1.65)	5.16 (2.02)	0.65 (0.48)	0.34 (0.08)	0.33 (0.07)	0.74 (0.26)
Rusty Crayfish	4.54 (1.51)	3.92 (2.03)	0.17 (n/a)*	0.33 (0.05)	0.40 (0.06)	1.0 (n a)*

*Standard error of the mean (SE) not applicable as only one sample obtained.

TABLE 3. Probability of capture by reproductive form and carapace length of Rusty Crayfish, *Orconectes rusticus*, associated with three stream sampling methods in 11 Ontario creeks: electrofishing, hand capture, and seining.

	Capture probability (mean [range])		
	Electrofishing	Hand capture	Seining
Reproductive form			
Form I male*	0.34 (0.26–0.54)	0.36 (0.33–0.39)	0.26†
Form II male*	0.46 (0.25–0.66)	0.36 (0.10–0.38)	0.20 (0.02–0.39)
Female	0.16 (0.06–0.28)	0.43 (0.14–0.57)	0.34 (0.32–0.35)
Carapace length			
< 10.5 mm	0.42 (0.38–0.45)	0.53†	n/a
10.5–20.4 mm	0.10 (0.01–0.19)	0.45 (0.19–0.62)	0.02†
20.5–30 mm	0.45 (0.27–0.62)	0.32 (0.09–0.44)	0.42 (0.29–0.54)
> 30 mm	0.33 (0.10–0.49)	0.70 (0.68–0.71)	0.62†

*Form I male = sexually active, form II male = sexually inactive.
†Single sample.

electrofishing and hand capture, a decline in catch was most frequently associated with form I males (63% and 50% of cases). Alternatively, seining declines occurred least often for form I males (17% of cases). Although based on a small number of samples, capture probabilities for male Rusty Crayfish were lower during seining than the other two methods, and for females lower during electrofishing (Table 3). There were no obvious differences among reproductive forms in capture probability by hand capture or seine. For electrofishing, capture probabilities tended to be greater for males (Table 3).

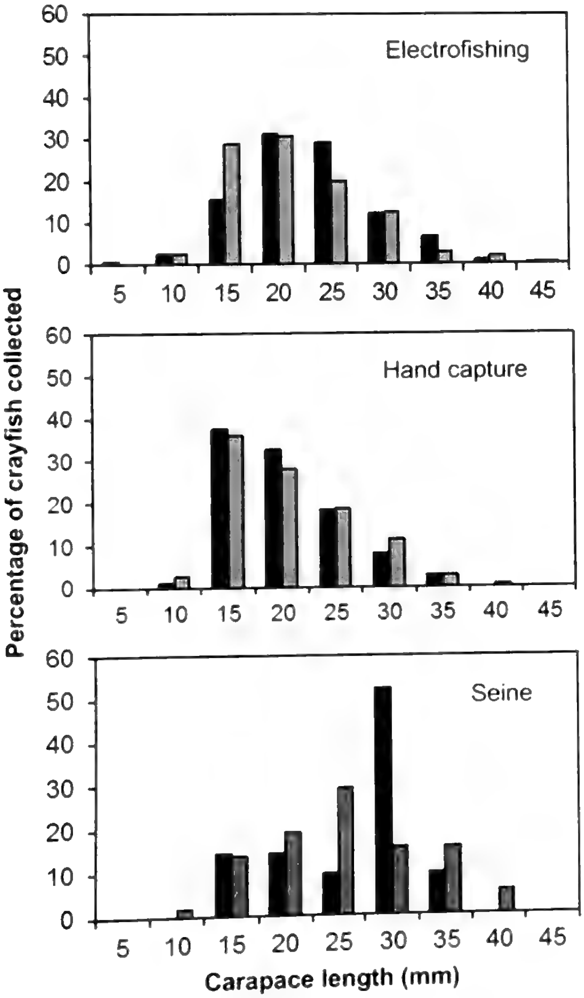

FIGURE 2. Distribution by carapace length of all crayfish species (black bars) and Rusty Crayfish, *Orconectes rusticus* (grey bars) captured by electrofishing, hand capture, and seining in 11 Ontario creeks.

Carapace length

A broad range of sizes of all crayfish species (CL range 5–43 mm) was collected during stream sampling (Figure 2). Electrofishing and hand capture resulted in a similar range of sizes, which included a greater proportion of small individuals (< 25 mm) than seining. However, CL distributions for samples collected by electrofishing and hand capture were significantly different (all species: $D = 0.15$; $P < 0.001$; Rusty Crayfish: $D = 0.13$; $P < 0.001$). Overall, hand-capture samples included a greater percentage of small individuals (CL 15–25 mm) than electrofishing.

For a third of samples, we were able to estimate capture probability for individual length classes. For hand capture and seining, a decline in catch was most frequently associated with larger Rusty Crayfish (CL 20–30 mm and > 30 mm). For electrofishing, declines occurred least often for the largest crayfish (CL > 30 mm), in only 18% of cases. Although based on a small number of samples, capture probabilities for most Rusty Crayfish length classes during hand capture were higher than other methods (Table 3). For electrofishing, capture probabilities were greatest for the smallest (< 10.5 mm) and the 20.5-30 mm length classes of Rusty Crayfish (Table 3). For the other two methods, differences in capture probability among length classes were also apparent. However, small sample sizes prevent meaningful comparisons.

Sampling injury

Cheliped loss was recorded for 8.8% of all crayfish collected by electrofishing, 6.3% by seine, and 5.4% by hand capture. Observed mortality was 1.4% for electrofishing and 2.2% for hand capture. No dead crayfish

of any species was observed during seining. Most dead crayfish were found either crushed or with a cracked carapace.

Discussion

All three sampling methods assessed in this study were effective at detecting Rusty Crayfish. Although multiple-pass sampling may improve detection of native species, it was not a reliable approach for estimating capture probabilities or population sizes of Rusty Crayfish and other crayfish species. In most cases, failure of the removal model was observed as an increase in the number of crayfish captured after the first pass or too few individuals collected. The first sampling pass may disturb or draw out crayfish from areas of cover making them more vulnerable to capture in subsequent passes (Gladman *et al.* 2010). Removal sampling by both electrofishing and hand capture has been suitable for generating population estimates of other stream-dwelling crayfish (Rabeni *et al.* 1997; Alonzo 2001); however, in those studies, sampling was carried out in much smaller streams and channel width can have a strong influence on efficiency of a method (Zalewski and Cowx 1990). To improve catch efficiency, Alonzo (2001) also used low voltage and activated the electrode for only 1–2 seconds at a time. In our study, we used voltage output and sampling strategies typical of stream fish inventories in Ontario. Although affected by electrical current, crayfish do not display the same degree of galvanotaxis as many stream fish. Experimentation with different settings could improve our capture efficiency.

Electrofishing and visual sampling methods are often biased toward capture of large individuals and against cryptic taxa or life stages (Zalewski and Cowx 1990). Activity levels and use of cover and deeper habitats vary among crayfish species, sizes, and reproductive forms (Berrill and Arsenault 1982; Guiasu 1997; Davis and Huber 2007) and, therefore, can also be expected to affect capture probabilities. For electrofishing, Alonzo (2001) reported a difference in the probability of capturing small and large crayfish in small streams, but none between sexes. In our study, the low number of removal estimates prevented robust comparisons of capture probability among reproductive forms and length classes. However, capture probabilities were generally higher for males during electrofishing and for the smallest and largest crayfish during hand capture. All three methods collected crayfish of different sizes, with seining providing a greater representation of large individuals. The large size of Rusty Crayfish associated with seine hauls from pools is consistent with Davis and Huber (2007) who observed that large Rusty Crayfish prefer deeper water than smaller individuals.

Although changes in the size of native crayfish populations after Rusty Crayfish introduction into lakes have been thoroughly documented, research on such declines in streams and rivers has been less intensive (Jezerinac 1982, 1991; Daniels 1998). Recent stream surveys in the mid-west and eastern regions of the United States indicate the continuing spread of Rusty Crayfish and concurrent declines in native *Orconectes* species (Kuhlmann and Hazelton 2007; Kilian *et al.* 2010; Lieb *et al.* 2011b; Olden *et al.* 2011). Based on a broad-scale survey of the Kawartha Lakes region, Berrill (1978) found the Rusty Crayfish to be widespread and common and indicated that it was likely replacing Northern Clearwater Crayfish. At our Kawartha Lakes stream sites, the Rusty Crayfish was the dominant (and often only) crayfish species present, indicating that the shift in species composition in this region has persisted for several decades. Jezerinac (1982) reported that location within the watershed influenced the effect of the Rusty Crayfish, with Northern Clearwater Crayfish abundant in headwaters and small tributaries (where few Rusty Crayfish were present) and absent or in low numbers in the main stream channel (where Rusty Crayfish were abundant). Although the expanding distribution of the Rusty Crayfish in southern Ontario has begun to be tracked, factors influencing its effect on native crayfishes in flowing waters are not well understood and require greater attention.

As the likelihood of species detection is improved, the use of multiple sampling methods has been recommended for crayfish surveys (Holdich *et al.* 2002). Backpack electrofishing and seining provide the best combination of methods to detect the Rusty Crayfish, native species, and a broad range of sizes of crayfish in Ontario streams. Although electrofishing was most effective at detecting both native and non-native species, seining is more suitable for sites that are turbid, deep, or have substrates too soft for effective electrofishing. Hand capture (or hand searching) does not require expensive equipment and is associated with fewer safety concerns than electrofishing. However, it was the most labour-intensive method, resulted in the highest rate of mortality, and is less readily adaptable to current stream fish monitoring programs. Gladman *et al.* (2010) and United States National Park Service (2007*) both reported hand capture to be less efficient than electrofishing for sampling stream crayfish.

As applied in this study, multiple-pass sampling was not a reliable strategy to estimate crayfish population size. However, multiple passes are still preferable to single-pass sampling as this improves native species detection (Gladman *et al.* 2010), and a large percentage of individuals will be vulnerable to capture only after being disturbed by initial sampling efforts. If estimates of population size are required for stream reaches, the likelihood of failure could be reduced by pooling data from randomly distributed sampling sites and applying unbiased removal-type estimators (Heimbuch *et al.* 1997). In this study, we did not estimate detection

probabilities for native crayfish. The design of stream monitoring efforts would benefit from additional studies that apply repeat survey designs (MacKenzie *et al.* 2002) to estimate method-specific detection probabilities.

Acknowledgements

This research was supported by the Ontario Ministry of Natural Resources and the Invasive Species Partnership Fund. J. Ciampa, S. Hogg, and M. Parna assisted with sampling. J. Rusak and K. Somers assisted with crayfish identification. The manuscript was improved with suggestions from D. McAlpine, K. Somers, E. Snyder, and two anonymous reviewers.

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Supplementary material available at:
http://www.canadianfieldnaturalist.ca

Received 12 September 2013
Accepted 9 February 2014

SUPPLEMENTARY MATERIAL:

TABLE S1. Crayfish catch data from each south-central Ontario stream sampling unit. For each method, electrofishing (EF), hand capture (HC), and seining (SN), the number of sampling passes is provided in parentheses. Note: Cb = *C. bartonii* (Appalachian Brook Crayfish), Oi = *O. immunis* (Calico Crayfish), Ob = *O. obscurus* (Allegheny Crayfish), Op = *O. propinquus* (Northern Clearwater Crayfish), Or = *O. rusticus* (Rusty Crayfish), and Ov = *O. virilis* (Virile Crayfish).

TABLE S2. Summary of catch data for Appalachian Brook Crayfish (*Cambarus bartonii*) and Northern Clearwater Crayfish (*Orconectes propinquus*) captured from Ontario streams using three methods: electrofishing, hand capture, and seining.

Estimating Breeding Bird Survey Trends and Annual Indices for Canada: How Do the New Hierarchical Bayesian Estimates Differ from Previous Estimates?

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Smith, Adam C., Marie-Anne R. Hudson, Constance Downes, and Charles M. Francis. 2014. Estimating breeding bird survey trends and annual indices for Canada: how do the new hierarchical Bayesian estimates differ from previous estimates? Canadian Field-Naturalist 128(2): 119–134.

Canadian data from the North American Breeding Bird Survey (BBS) provide information on the population status and trends for over 300 species that regularly breed in Canada. Since the first assessments were made in the mid-1970s, both the dataset and the suite of statistical tools and techniques available to researchers have grown. As a result, Canadian BBS trend estimates have been derived from numerous statistical models. Because the BBS data are relatively complex, different statistical models can generate different trend and status estimates from the same data. In 2013, Environment Canada's Canadian Wildlife Service began producing BBS status and trend estimates using a hierarchical Bayesian model. To give users of BBS trends and annual indices of abundance a better understanding of these estimates, we demonstrate and explain some of the similarities and differences between the new hierarchical Bayesian estimates and those from the previous model; discuss the philosophical and inferential consequences of estimating trends with the new model; and describe how the hierarchical Bayesian model differs from the model currently used in the United States. Overall, trends and annual indices from the new model are generally similar to estimates from the previous model; however, they are more precise, less variable among years, better represent the spatial variation across Canada in population status, and allow for more intuitive and useful assessments of uncertainty.

Key Words: breeding bird survey; hierarchical Bayesian model; maximum likelihood model; population trend; population monitoring

Introduction

The North American Breeding Bird Survey (BBS) provides information on the population status (trends and annual indices of abundance) of almost 300 bird species in Canada. Indeed, it is the primary source of information for over 200 of those species. Due, in part, to its long history and continental coverage, the BBS is considered to be the backbone of land bird conservation in North America (Rich *et al.* 2004*). It is a vital component of a wide variety of high-level conservation documents for Canada, e.g., the State of Canada's Birds (North American Bird Conservation Initiative Canada 2012*) and the Status of Birds in Canada website (Environment Canada 2011*). Data from the survey have also been used in hundreds of scientific publications on topics ranging from assessing population trends to modelling habitat associations or impacts of climate change on range shifts (Pardieck *et al.* 2008).

The approaches used to analyze BBS data have evolved over time as new statistical methods have become available and as the dataset has grown to support increasingly complex models. The first Canadian BBS routes were conducted in 1966, and the first national trend estimates included the data from the first 10 years (Erskine 1978*). Population trends in that report were estimated using a chaining-style analysis of averaged year-to-year changes in species counts on routes run in successive years, with the chain of year-to-year changes indexed to a value of 100 in a base year (1973). Subsequently, both the Canadian Wildlife Service (CWS) and the United States Geological Service (USGS) began to analyze the BBS data annually, but using different methods. Early analyses by the United States' agencies (at the time, the Fish and Wildlife Service) calculated annual indices using weighted average counts across years and trends using route-regression models (Robbins *et al.* 1986). Through the 1980s and 1990s, various route-regression models (Geissler and Noon 1981) were used by both the CWS and USGS, although variation in approaches to weighting routes led to different estimates (Thomas and Martin 1996). The USGS analyses continued to use route-regression models through 2008, while, from 2002 to 2009, Canadian BBS data were analyzed using a maximum likelihood (ML) model, which estimated an annual index. Starting with the 2011 BBS data, Canadian trends and annual indices have been estimated using a hierarchical Bayesian (HB) model, which is very similar to the model adopted by the USGS in 2009 and described in Link and Sauer (2002) and Sauer and Link (2011).

HB methods suit the BBS data's complex structure, because the Bayesian framework provides a coherent and flexible approach for modelling the effects of sampling variation (e.g., not all routes are surveyed each year; not all birds present on a route are detected on any given survey; and detection probabilities vary among

observers) separately from temporal and geographic variation in the underlying populations (e.g., population change due to changing weather, resource abundance, and human activity). In addition, the hierarchical structure is particularly efficient and powerful because the distributional assumptions of the random effects greatly reduce the number of parameters that need to be estimated to model observer effects and other nuisance parameters (Clark 2005). Similarly, the hierarchical structure of the model mirrors the hierarchical structure of the data and allows effects to be modelled at the appropriate scale, e.g., nuisance parameters, such as overdispersion and the effects of changes in observers over time, can be efficiently modelled across all counts, while trends and annual variation around the trend can be modelled across routes within strata (Link and Sauer 2002).

Bayesian methods also provide intuitive and direct estimates of the uncertainty around the population parameters (i.e., population trends and indices of annual abundance) that are of primary interest to most users. Bayesian methods are based on the idea that our understanding of an imperfectly known parameter, such as a population trend, has a probability distribution. That is, the mean, median, or mode of the distribution is our best estimate of the parameter, and the variance, standard error, or percentiles (i.e., the credible interval) of the distribution represent the uncertainty around our best estimate. Our initial understanding of that distribution is termed the prior probability distribution. The data are used to update the prior probability distribution, through Bayes' rule, to produce the posterior probability distribution, which expresses our final understanding of the parameter (Link and Barker, 2009). For example, with a Bayesian framework, it is relatively simple to estimate the posterior distribution of the total change in a population since 1970, and from that distribution, make concise and direct statements about the probability that a population has declined; whereas with previous analyses, uncertainty estimates were largely limited to probabilities of observing the data (or more extreme data) if the true population had not changed.

The differences between Bayesian and frequentist (i.e., traditional) estimates of uncertainty are exemplified in comparing Bayesian credible intervals with frequentist confidence intervals. Credible intervals provide a probable range of values for a parameter (e.g., in the case of a 95% credible interval, the range of values that contains, with a 95% probability, the true value of a population trend). Many readers will be more familiar with confidence intervals and likely with interpreting them in the same way. However, for confidence intervals this interpretation is incorrect, and the confusion largely stems from the unintuitive nature of the true definition of confidence interval, which relates to an infinite number of hypothetical realisations of the data (Clark 2005). In essence, credible intervals, and Bayesian methods in general, provide intuitive and useful measures of uncertainty. For example, the current BBS results website maintained by Environment Canada (www.ec.gc.ca/ron-bbs) provides, for every trend estimate, associated estimates of the probabilities of eight thresholds of population change (e.g., probability that the population has decreased, increased by > 100%, etc.). Species-at-risk status assessments can now easily consider an explicit measure of the probability that a population has reached one of the thresholds used to categorize a species as threatened or endangered (e.g., COSEWIC 2011*).

The application of HB methods to the BBS represents the most recent development in estimating the status and trends of hundreds of bird species across North America. Three closely related HB models are described in the literature or are in use for analyzing trend and annual indices from the BBS data. The first model (HB_1) was described by Link and Sauer (2002). It was subsequently refined to account for the bias in retransforming annual index estimates from the log-scale to the scale of average counts (second equation in Sauer and Link 2011). The second model (HB_2) is currently used in annual analyses by the USGS. The third model (HB_3) includes an additional refinement that has the effect of scaling the annual indices more closely to the average observed count on routes within a stratum and improving estimates of trends for larger regions. HB_3 is the model currently used in the CWS annual analyses. The distinction between models HB_2 and HB_3 is important because trend and annual index estimates from the USGS include Canada and Canadian provinces. Therefore, anyone interested in a species trend for Canada must choose between the estimates derived by the USGS (using model HB_2) and those derived by the CWS (using model HB_3).

Because the BBS data and the statistical models used to analyze them are complex, different analytical approaches can result in different estimates of population parameters, particularly if the underlying signals in the data are relatively weak or variable or if the sampling is imbalanced. The BBS sampling method is a stratified random design that aims to generate a balanced and approximately representative sample of bird populations across North America (Erskine 1978*). Of course, as with any field survey, practical constraints introduce some variation and bias into the data: uneven spatial distribution of active routes, changes in the number and spatial coverage of routes surveyed over time, and variation among and changes over time in observers. The nested structure of the data (i.e., stops nested within routes, routes selected within degree-blocks and aggregated into analytical strata) provides added challenges. Analyses of BBS data have different ways of accounting for all or some of these sources of variation and bias, and, as a result, different analyses can

sometimes generate different estimates of population trends and annual indices (e.g., Thomas 1996; Thomas and Martin 1996; Sauer and Link 2011).

For many species and regions, the underlying signals in the data are clear and strong, the sample sizes are large, or the BBS sampling is very well balanced in space and time. In these cases, even very different models will generate similar estimates of population status and trends. In addition, although point estimates of trend for a given species and region may differ among models, most conservation or management decisions and actions are based on relatively broad overall patterns in population status. For example, the Status of Birds in Canada website classifies species based on six categories of population status, such as large decrease, moderate increase, little change, and data deficient (Environment Canada 2011*). Each of these categories encompasses a relatively wide range of trend values; thus, even when point estimates of trend or trajectory differ among models, the broad population inferences may be similar, particularly for populations with relatively extreme status (i.e., large decrease or large increase), which are likely to be the primary focus of management.

Our three goals in this paper are to describe in detail the HB_3 model we are now using in Canada to estimate population trends and how it differs from the HB_2 model used by the USGS; to demonstrate and explain some of the similarities and differences in the estimates provided by the HB_3 model and the previous Canadian model (the ML model); and to discuss the most important philosophical and inferential consequences of estimating trends and annual indices of abundance with the HB_3 model.

Methods

Maximum likelihood model

The model used to generate Canadian BBS trends between 2002 and 2009 is a weighted ML model (see Appendix 1). It uses a series of equations to derive ML estimates of stratum and year-specific annual indices ($\lambda_{i,j}$):

$$\lambda_{i,j} = \exp\left(\mu + \alpha_i + \beta_j + \gamma_{j,k}\right)$$

The model assumes counts of birds on BBS routes are Poisson distributed, and estimates terms to account for the effects of each year (β_j), variation among routes (α_i), and variation among observers and observation conditions in each year ($\gamma_{j,k}$). The means of the estimated effects of year, route, and observer are fixed at 0, and μ is not estimated, but held constant as the observed average count of birds across all years and routes. The analysis is conducted using the sampling strata of the survey: degree blocks (regions defined by one degree latitude and one degree longitude, Figure 1 inset). The ML estimation of annual indices is weighted so that each degree block with data influences the estimate in proportion to its area, regardless of the number of routes with data. Weighting limits the influence of degree blocks with more routes, which, because the BBS is volunteer-based, tend to occur in areas with larger human populations. The weight for each route from degree block i used in the analysis is $n_i^{-1} * Ai$, where n is the number of routes in the degree block and A is the degree block's area. The model was run through a custom C++ program.

The ML model estimates the annual indices directly, and trends are derived from log-linear regressions of the annual indices of abundance. A small constant (0.001) is added to the annual indices before the log-linear regression, because in years when the species is not observed the annual index is set to 0. The standard errors of the abundance indices and trends are estimated using a "jackknife" procedure, which discards one route at a time. A full description of the model has never been published; however further details are provided in Appendix 1.

Hierarchical Bayesian model, HB_3

The CWS is now generating Canadian BBS trends using the HB_3 model. It assumes that observed counts on a BBS route j in year t and stratum i have a Poisson distribution with mean ($\lambda_{i,j,t}$). The strata used are areas created by the intersection of provincial and territorial boundaries with those of the North American Bird Conservation Regions (BCRs; North American Bird Conservation Initiative International 2013*; Figure 1). On the log scale, the λs are modelled by fixed effects for first-year observer effects (η, where the value of $\mathbf{I}(j,t)$ is 1 if a route–year combination represents an observer's first year on that route and 0 otherwise) and stratum-specific fixed effects for abundance (S_i), trend over time (β_i), and variance of the year effects within each stratum ($\sigma^2_{\lambda_i}$). The model also has random effects for overdispersion ($\varepsilon_{i,j,t}$) of counts and stratum-specific random terms for year effects ($\lambda_{i,t}$) and observer–route effects ($\omega_{i,j}$).

$$\log(\lambda_{i,j,t}) = S_i + \beta_i * t + \gamma_{i,t} + \omega_{i,j} + \eta\mathbf{I}(j,t) + \varepsilon_{i,j}$$

[equation 1]

All prior distributions are standard, diffuse (non-informative) conjugate priors; that is, the priors are chosen so that the estimates are not influenced by any prior knowledge—non-informative—and the specific distributions, such as the inverse gamma for variances, ensure proper posterior distributions—conjugate priors. Specifically, all variances are assigned diffuse inverse gamma prior distributions (scale and shape parameters set to 0.001) and the parameters S, β, γ_t, and η are given diffuse normal distributions (mean 0, variance 10^6).

The annual indices of abundance for stratum i and year t are exponentiated sums of the year, stratum, and trend effects estimated in equation 1, scaled by the proportion of routes in the stratum on which the species was observed (z_i).

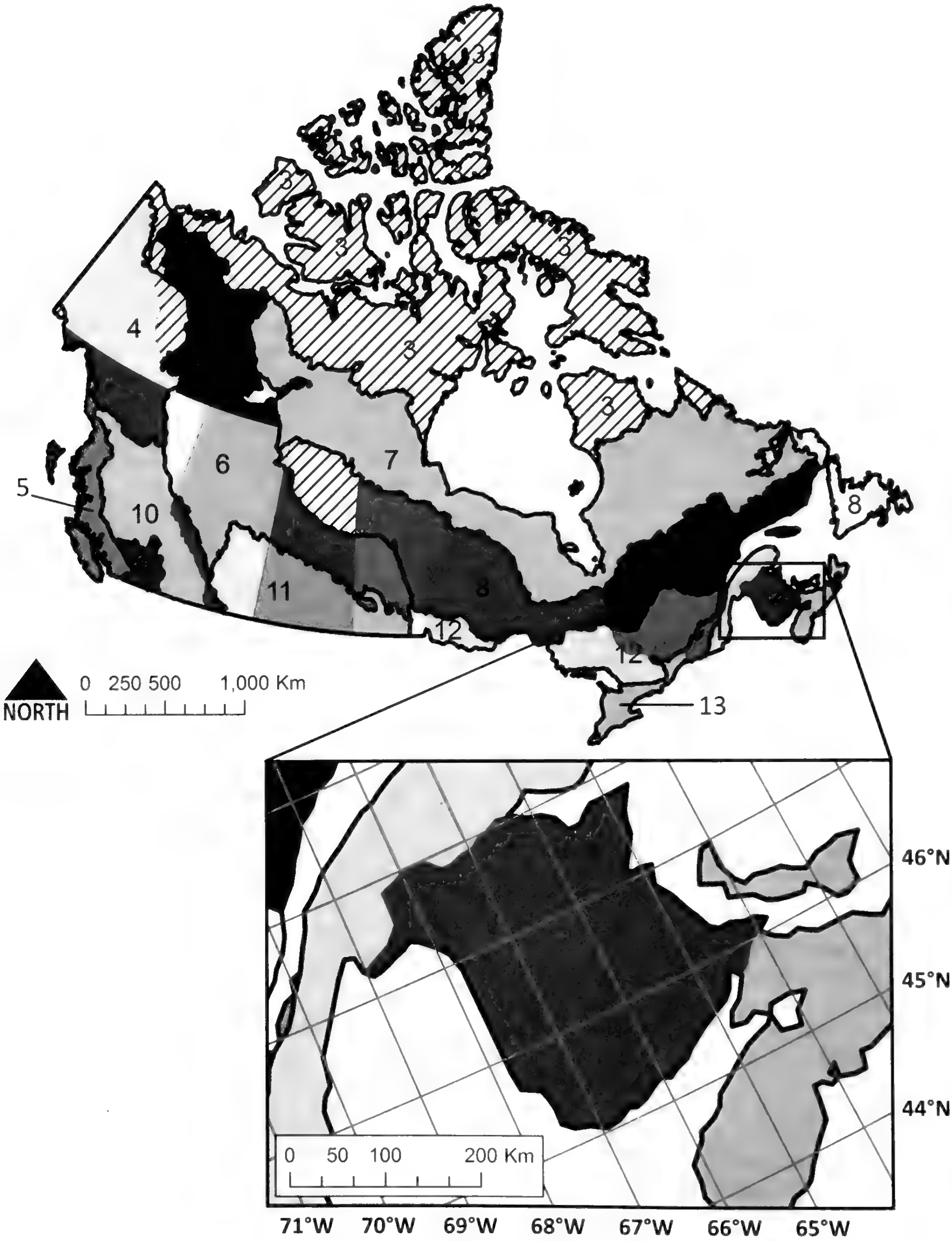

FIGURE 1. Geographic strata for analysis of Breeding Bird Survey (BBS) data using the Canadian hierarchical Bayesian model. The strata are the areas created by the intersection of provincial and territorial boundaries with those of Bird Conservation Regions (BCRs). Exceptions are the strata consisting of all of BCR 7, which crosses several provinces and territories, and all of BCR 14, which includes Nova Scotia and Prince Edward Island. BCR borders are indicated by heavy black lines: BCR 3, Arctic Plains and Mountains; BCR 4, Northwestern Interior Forest; BCR 5, Northern Pacific Rainforest; BCR 6, Boreal Taiga Plains; BCR 7, Taiga Shield and Hudson Plains; BCR 8, Boreal Softwood Shield; BCR 9, Great Basin; BCR 10, Northern Rockies; BCR 11, Prairie Potholes; BCR 12, Boreal Hardwood Transition; BCR 13, Lower Great Lakes/St. Lawrence Plain; and BCR 14, Atlantic Northern Forest. Within provinces and territories, strata are indicated by different shades of grey. Regions filled with diagonal lines have insufficient BBS data to be included in any analyses. The inset shows the original sampling strata for the BBS, i.e., degree-blocks, overlaid on the province of New Brunswick.

$$n_{i,t} = z_i * e^{S_i+\beta_i*t+\gamma_{i,t}+0.5*\sigma^2_{\omega_i}+0.5*\sigma^2_\varepsilon}$$

[equation 2]

The variance components ($0.5 * \sigma^2_{\omega_i} + 0.5 * \sigma^2_\varepsilon$) are added to correct for retransformation bias: the exponent of the average of a normal distribution – the sum of $S_i + \beta i * t + \gamma_{i,t}$ – underestimates the average of the log-normal distribution (Newman 1993). The variance components ensure that the indices are scaled to an average number of birds per route. Annual indices for larger regions, i.e., provinces, territories, BCRs, or country, are area-weighted sums of the stratum-level estimates:

$$N_t = \frac{\sum A_i * n_{i,t}}{A}$$

[equation 3]

Trends in the HB_3 model are estimated as geometric mean annual changes in population size over specific intervals, expressed as a percentage. That is, the trend B from year t_a to year t_b for a given region is:

$$\bar{B} = 100 * \left(\left(\frac{N_{t_b}}{N_{t_a}}\right)^{\frac{1}{t_b-t_a}} - 1\right)$$

[equation 4]

The HB_3 model described here is very similar to the HB_2 model used by the USGS (described in Sauer and Link 2011) with one modification: the HB_2 model estimates a common observer–route variance across all strata (σ^2_ω instead of $\sigma^2_{\omega_i}$). In the HB_3 model, the stratum-specific observer–route variances ($\sigma^2_{\omega_i}$) are drawn from a hyperdistribution that allows the variance of observer–route effects to differ among strata and yet be estimated relatively efficiently, even for strata with relatively few observer–route combinations. The hyperdistribution is defined such that the precision (the inverse of the variance) of stratum-specific observer–route effects ($1/\sigma^2_{\omega_i}$), is assumed to come from a log-normal distribution with a common mean and variance, i.e., $\log(1/\sigma^2_{\omega_i}) = N(\mu_\zeta),\sigma^2_\zeta)$. In comparison, the HB_2 model estimates a single observer–route variance term (σ^2_ω) across all observer–route combinations, which is given a diffuse inverse gamma prior distribution (scale = shape = 0.001). The WinBUGS code for the HB_3 model is available in Appendix 2A.

Comparisons between models

We used the HB_3 and ML models to estimate trends and annual indices for all species using a common dataset. The dataset included all observations from Canadian BBS routes, run from 1970 through 2011, under acceptable observation conditions (i.e., coded as RunType = 1; USGS 2012*). Although the original datasets were identical, the models have slightly different inclusion criteria for a given route–year combination. For example, the ML model estimates a route-specific trend parameter that requires a minimum of 2 years of observations on each route, whereas the HB_3 model estimates a stratum-specific trend parameter and, therefore, can include data from routes with only 1 year of data. These differences were relevant to very few route–year combinations (< 1%), so they resulted in only very small differences in the final estimates. All species names (English, French, and scientific), as well as all trend estimates for each species, region, and trend period, are available in Appendix 3.

For most comparisons, we contrasted estimates from the two models at three scales. First, the national scale provides a comprehensive comparison that has relevance to many conservation and management decisions. Second, the BCR-scale comparisons highlight some of the important spatial characteristics of each model, e.g., differences in area weights, spatial scope of inference, and minimum data criteria (Canada's 11 BCRs are shown in Figure 1). Finally, a comparison for one province (New Brunswick; Figure 1 inset), which is an identical stratum in both analyses, provides the most direct comparison. This last comparison highlights differences between the overall frameworks of the ML and HB_3 models, because the data, spatial extent, and relative area weights are as similar as possible.

We made quantitative comparisons of five characteristics of the two models: (1) the number of species in each region with trend estimates, (2) the magnitude of trends, both long term (> 40 years) and short term (10 years), (3) the precision of trend estimates, (4) the inter-annual variability of short-term trends, and (5) the scale of the annual indices. We did not include a comparison of the number of statistically significant trends in the two models (i.e., a trend estimate for which the confidence or credible interval excludes zero). Statistical significance is a synthetic metric that confounds trend magnitude and precision; therefore, making such a comparison would add nothing new to the comparisons made here.

Magnitude of trends: To compare the magnitude of the long- and short-term trends, we used an HB model analogous to a weighted paired t-test that accounts for the uncertainty of each individual trend estimate. Extreme trend estimates (i.e., estimates that are larger in absolute magnitude) are more likely to be imprecise and would strongly influence a direct comparison of trends if not weighted by precision. Our comparison approach was derived from one originally described in Sauer and Link (2002), which assumes that estimated trends are part of a collection of trends that share a common mean and variance. However, we did not assume a common average trend for each model (as suggested in Link and Barker 2009) and did not, therefore, shrink imprecise estimates toward a common mean. The comparison model uses trend estimates ($\beta_{s,m}$, trend estimates for species s from model m) as data and accounts for uncertainty in the estimation of those trends using estimates of the variance of each

trend ($\sigma^2_{s,m}$). It makes pairwise, within-species comparisons between the posterior estimates of trend from each model

$$(\beta_{s,HB} - \beta_{s,ML})$$

and compares the overall average species-specific differences

$$(\frac{\sum_1^S \beta_{s,HB} - \beta_{s,ML}}{S}).$$

The comparison model estimates the average, species-level difference (i.e., the result of subtracting one estimate from another) in trends between the two models, weighted by the relative precision of each estimate. The average of the species-level differences is an estimate of the relative bias in the two models: positive differences indicate that the HB_3 trend estimates tend to be more positive (less negative) than the ML trend estimates for a given species. In addition to evaluating bias, we also estimated the correlation coefficient of species-level posterior trend estimates from this model, as a measure of overall agreement between trends estimated by the two models. The WinBUGS code for the comparison model is provided in Appendix 2B.

To compare the tendency for each model to produce extreme trend estimates (i.e., larger in absolute magnitude), we estimated the slope of a regression of ML trends on HB trends, using major axis, model II regression methods (Legendre and Legendre 1998). Slope values > 1 would indicate that, on average, trends from the ML model are more extreme for a given species. Values < 1 indicate that HB trends are more extreme. We used an unweighted regression, because precision-weighted comparisons would greatly reduce the influence of the extreme trends, which are often imprecisely estimated.

Precision of trends: To compare the precision of trend estimates between the two models, we treated credible intervals for the HB_3 model and confidence intervals for the ML model as comparable estimates of variance (Sauer and Link 2011). Despite their fundamental mathematical and philosophical differences, 95% credible intervals from simple Bayesian models using diffuse priors are generally very similar to 95% confidence intervals from comparable frequentist models and, in practice, they are used in similar ways to assess uncertainty in model estimates (Clark 2005). We used the model described for comparing the magnitude of trends to simultaneously compare the precision of trend estimates

$$(\frac{1}{\sigma^2_{s,m}}).$$

This model accounts for both the imprecision of each trend estimate (through the estimated variance of trends) and the imprecision around the estimate of the variance. Specifically, the model assumes that the estimated variances ($\hat{\sigma}^2_{s,m}$) of each trend estimate are mutually independent (both within species [s] and within models [m]) and independent of their associated trend estimates (Sauer and Link 2002). The true variance of each trend ($\sigma^2_{s,m}$) was estimated using a chi-squared distribution with n degrees of freedom, such that

$$\frac{n * \hat{\sigma}^2_{s,m}}{\sigma^2_{s,m}} \sim \chi^2_n,$$

where n is the number of routes on which the species was observed (i.e., the number of routes contributing data to the trend analysis). We then estimated the proportion of species for which the HB_3 trend was more precise (i.e., $\sigma^2_{s,HB} < \sigma^2_{s,ML}$) and the average pairwise differences in the standard errors of each species' trend

$$(\frac{\sum_1^S \sigma^2_{s,HB} - \sigma^2_{s,ML}}{S}),$$

where S is the number of species.

Inter-annual variability in short-term trends: The two models have very different definitions of trend (Sauer and Link, 2011): the HB_3 model estimates trend as an endpoint comparison of the annual indices in the first and last years of a given period; the ML model estimates a series of annual indices, then derives trend as the slope of a log-linear regression of the indices against time. Because the HB_3 model trend estimate is an end-point comparison, which does not directly include any of the indices in the intervening years, trend estimates from the HB_3 model could be more variable among consecutive years (i.e., greater inter-annual variation). For example, consecutive 10-year trends estimated using the HB_3 model (e.g., 2000–2010 and 2001–2011) are based on completely different pairs of annual indices. Variability of this sort is particularly important because these short-term, 10-year trends are the basic estimates of population change used for species assessments by COSEWIC. Undue inter-annual variation in trends could introduce some uncertainty and instability into important and potentially costly conservation decisions.

To compare inter-annual variation in short-term trends, we calculated all possible 10-year trends ($\beta_{\text{year } x - \text{year } x+10}$) using each model from the entire time-series of BBS data, i.e., $\beta_{1970-1980}$, $\beta_{1971-1981}$, …, $\beta_{2001-2011}$. We then calculated the absolute value of the change in estimates between all 32 consecutive pairs of trends, e.g., $\Delta\beta_1 = |\beta_{1970-1980} - \beta_{1971-1981}|$, $\Delta\beta_2 = |\beta_{1971-1981} - \beta_{1972-1982}|$, …, $\Delta\beta_{32} = |\beta_{2000-2010} - \beta_{2001-2011}|$. We averaged these estimates of consecutive change in trend across the full time series

$$(\overline{\Delta\beta} = \sum_{i=1...32} \Delta\beta_i / 32)$$

and compared the averages between the ML and HB_3 models for each species at the national scale.

Scale of annual indices: The annual indices from the BBS reflect the relative abundance of a species

among regions and influence the relative weight of each region's population trend in composite trends for larger regions. In addition, the indices are used in many conservation documents as a scale of the relative abundance among species. In regions that are identical in the two analyses, the two models produce annual indices of abundance on the same scale — the average expected count on an average route, conducted by an average observer. However, annual indices from the two models are derived in fundamentally different ways. The ML model estimates the annual indices directly, and trends are derived from log-linear regressions of the indices on year. The HB_3 model estimates trends directly and annual indices are derived estimates of departures from a long-term trend line. We compared the scaling of annual indices from the two models for a region that is identical in the two analyses — New Brunswick. For each species, we calculated the average of the annual indices from each model for New Brunswick for 1985–1995, which roughly represents the middle of the time series for the BBS in Canada. We limited our quantitative comparison to this one region and window of time because it provided the most direct comparison. It was largely unaffected by differences among strata in area weights, the inclusion or exclusion of particular routes, or in the indices at either end of the time series, which are more likely to be influenced by the way in which the ML model handles years with no observations or by strong underlying trends estimated using the HB_3 model.

To quantify differences in the scale of annual indices, we used a generalized linear mixed model with a Gaussian error distribution, a log-link, a fixed effect of model type (HB_3 vs. ML), and a random effect for species. We used the log-link because the models that produce the annual indices estimate the variances of the indices on the log scale and so that we could provide each species with an approximately equal weight in the analysis (i.e., comparing estimates on the linear scale would give abundant species undue weight). We report the retransformed parameter estimate and confidence intervals for the fixed effect of model type as the average difference in annual indices between the two models.

The HB_3 model used here produces annual indices on a slightly different scale than the HB_2 model, which estimates a single observer–route variance term for all strata (σ^2_{ω}). Therefore, we also compared annual indices from the HB_2 model with indices from the ML model. Observer–route variance influences the scaling of annual indices in both HB models in two ways. First, the structure of the observer–route variance (σ^2_{ω} vs. $\sigma^2_{\omega_i}$) affects the estimates of the average stratum-level abundance (S_i). Second, the estimates of observer–route variance are used as a retransformation factor that scales the annual indices to an estimate of average counts per route.

If a common observer–route variance across all strata is estimated, as in the HB_2 model, some of the ecologically relevant variation in abundance among strata is modelled as observer–route error and not incorporated into the estimates of S_i, which, as a result, become more similar among strata, i.e., they approach the survey-wide average abundance. The observer–route variance estimate is composed of the variation in abundance among individual BBS routes as well as the variation among observers. Although the variance among observers is entirely a source of error, the variance among routes represents, at least partly, ecologically-relevant spatial variation in abundance. This spatial variation in abundance among routes is also nested within the variation in abundance among strata — routes are uniquely associated with a given strata. As a result, when a common observer–route variance is estimated (σ^2_{ω} in the HB_2 model), some of the variation in abundance among routes is modelled as error. By contrast, the stratum-specific estimates of observer–route variance ($\sigma^2_{\omega_i}$ in the HB_3 model) allocate more of the variation in abundance among strata to the estimates of S_i.

The stratum-specific variance estimates in the HB_3 model also retain greater variation in abundance among strata, because they provide stratum-specific retransformation factors to rescale the annual indices. The observer–route variance is one of two variance components ($0.5 * \sigma^2_{\omega_i}$ in equation 2) that are added to the parameter estimates on the log-scale to adjust for the bias in transforming from the log scale to the linear scale (i.e., count of birds). Annual indices in the HB_3 model are scaled by a multiplicative function of $e^{0.5*\sigma^2_{\omega_i}}$, which varies among strata; the analogous function ($e^{0.5*\sigma^2_{\omega}}$) is the same for all strata in the HB_2 model.

All figures that include comparisons of the ML and HB_3 models at the BCR scale have been arranged so that the BCRs are sorted in descending order of an approximate estimate of data quality, i.e., BCRs are sorted in descending order of

$$\frac{\sqrt{n_b}}{A_b}$$

for each BCR, b, where n_b is the number of routes and A_b is the area of the BCR. Some additional comparisons are included in Appendix 4.

Results

Magnitude of trends

Overall, trends estimated from the ML and HB_3 models were generally similar. Estimates from the two models were correlated for all regions and time periods (Figure 2), with higher correlations at the level of individual strata and BCRs than at the national level (compare plots for Canada and New Brunswick in Figure 2 and Figure 3A). Long-term trends were generally more correlated than short-term trends (Figure 3A). Trends

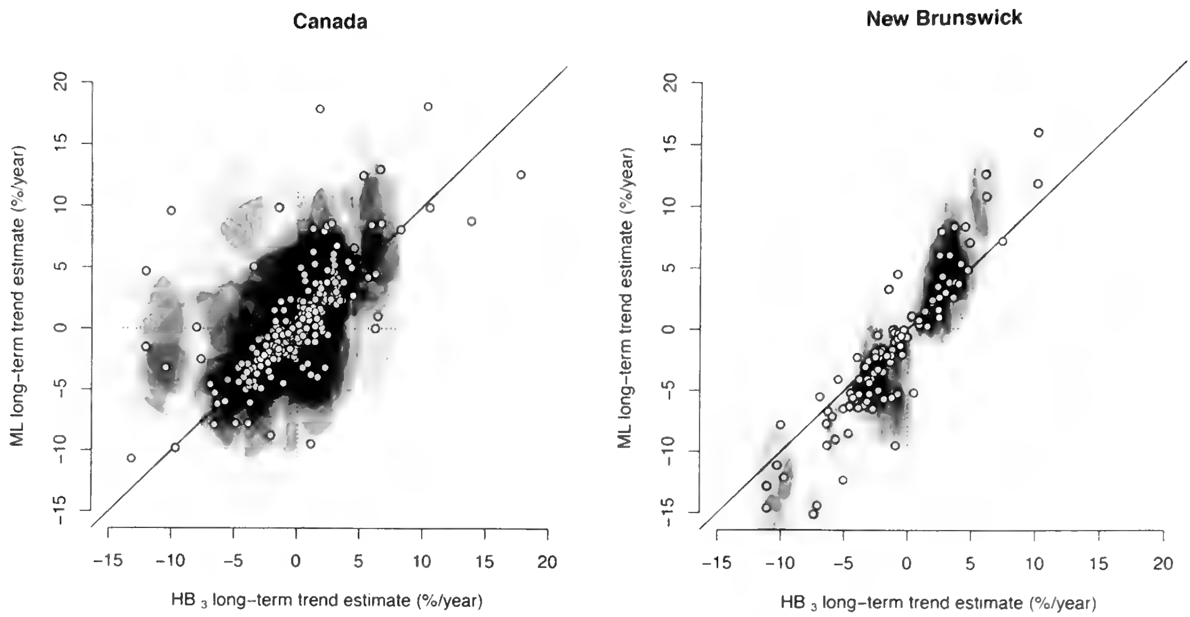

FIGURE 2. Point estimates (circles) and associated uncertainty (semi-transparent ellipses) of long-term Breeding Bird Survey trends for Canada and New Brunswick calculated from the previously used maximum likelihood (ML) model and the new hierarchical Bayesian (HB_3) model. The diameters of the ellipses represent the central 67th percentile of the posterior distribution of trend estimates from the Bayesian trend comparison model (vertical diameter = ML trend estimates and horizontal diameter = HB_3 trend estimates). The diagonal line indicates a 1:1 relationship. The dotted black lines divide the plot into quadrants representing combinations of trend–signs from the two models (e.g., points and posterior mass plotted in the upper right quadrant represent species with positive trend estimates from both models). Differences in trends for Canada incorporate differences between the two models in terms of model structure and assumptions, as well as differences in area weights, routes, and regions of the country included in the estimates. Differences in trend estimates for New Brunswick are almost entirely due to differences in model structure and assumptions. One species was omitted from both graphs because its trend estimates were extreme (> 25%/year) and including it changed the scale such that it became difficult to discern relations among the remaining species.

from the two models also tended to be more correlated in regions with more data (i.e., BCRs closer to the left side of Figure 3A, which have more routes in relation to their area).

At the national level, 54% of species had HB_3 trends that were more negative than their ML trends, and HB_3 trends were on average slightly more negative: the average species-level difference in long-term trends was −0.26%/year, although the 95% credible interval—the interval between the 2.5 and 97.5 percentiles of the posterior distribution—included zero (−0.68 to 0.16; Figure 3B). In contrast, national short-term trends from the HB_3 model were on average more positive: 64% of species had HB_3 trends that were more positive, and the average difference was 1.1%/year, (95% credible interval −0.41 to 1.7; Figure 3B). For most BCRs, the average differences between trend estimates from the two models followed the same pattern observed in the national estimates, i.e., the differences in long-term trends were more often negative and differences in short-term trends were more often positive (open circles below the dotted line and closed circles above in Figure 3B).

All trends from the HB_3 model tended to be less extreme (i.e., less in absolute magnitude, points above the dotted line in Figure 4), except for the national long-term trends, where the opposite was true.

Precision of trends

Trend estimates from the HB_3 model, both long- and short-term, were more precise than estimates from the ML model in all regions. For national trends, 63% of species had more precise trends with the HB_3 model, and the standard errors of HB_3 trends averaged approximately 0.5%/year smaller than the standard errors of the ML trends (Figure 5). Within the BCRs, HB_3 trends were more precise for almost all species (73–98%) and their standard errors averaged approximately 2%/year smaller (Figure 5).

Inter-annual variability of short-term trends

Ten-year trend estimates from the HB_3 model were generally less variable among years than those from the ML model (Figure 6). Across species, the mean absolute year-to-year change in 10-year trend estimates was 1.12%/year smaller using the HB_3 model than the ML model for a given species. The average species-level difference (HB_3 _ ML) in the mean absolute year-to-year change in national 10-year BBS trends was −1.12 (SE 0.17); in Figure 6A, most points are to the right of the 1:1 diagonal line. In general, 10-year trends

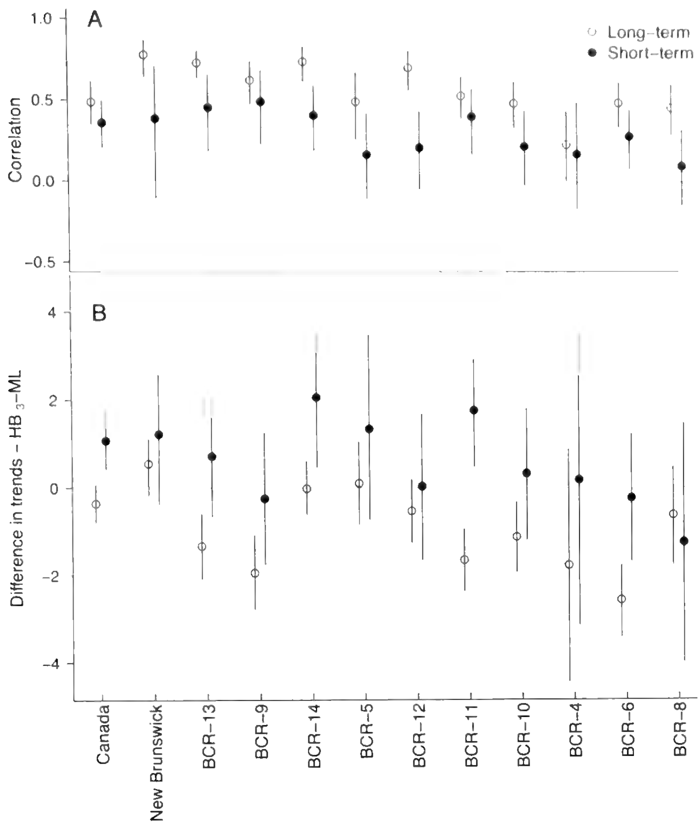

FIGURE 3. Correlation and comparison of the magnitude of long- and short-term Canadian Breeding Bird Survey trends estimated using the earlier maximum likelihood (ML) model and the new hierarchical Bayesian (HB_3) model. Bird Conservation Regions (BCRs) are arranged in descending order of the ratio of the square root of sample size to area. The correlations plotted in the upper graph show the overall similarity of trends estimated using the two models. The differences plotted in the lower graph show the relative bias in the two models: negative values indicate that the HB_3 trend estimates were smaller than the ML estimates (i.e., the population change was more negative and/or less positive); positive values indicate the opposite. All comparisons were made on the posterior estimates of trends, output from a model that accounts for the relative precision of the original estimates. The circles represent the means of the posterior distribution, with error bars indicating 95% credible intervals. See Figure 1 for BCR definitions.

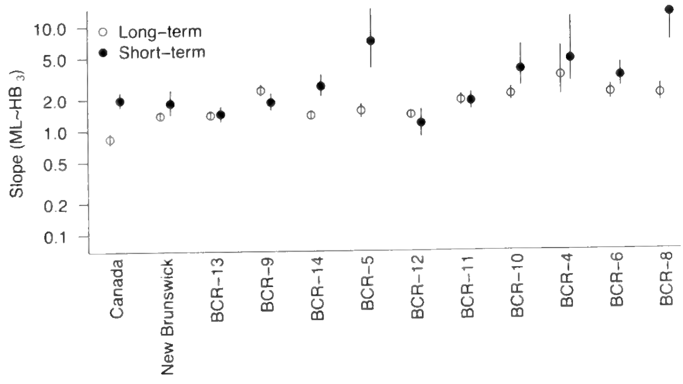

FIGURE 4. Slopes of major axis, model II regressions of Breeding Bird Survey trend estimates from the previously used maximum likelihood (ML) model regressed on estimates from the new hierarchical Bayesian (HB_3) model. Bird Conservation Regions (BCRs) are arranged in descending order of the ratio of the square root of sample size to area. These comparisons do not consider the precision of the estimated trends, for reasons explained in Methods. Values > 1.0 indicate that the absolute values of the ML trends are, on average, more extreme than the HB_3 trends for each species (i.e., the ML trends are larger in absolute magnitude) and values < 1.0 indicate that the HB_3 trends are more extreme. Error bars indicate 95% confidence intervals for the slope estimates. Slope values are plotted on a logarithmic scale so that equal deviations from the 1:1 expectation appear equal above and below the dotted line (e.g., a slope of 2.0 represents the same magnitude of deviation from the expectation as a slope 0.5). See Figure 1 for BCR definitions.

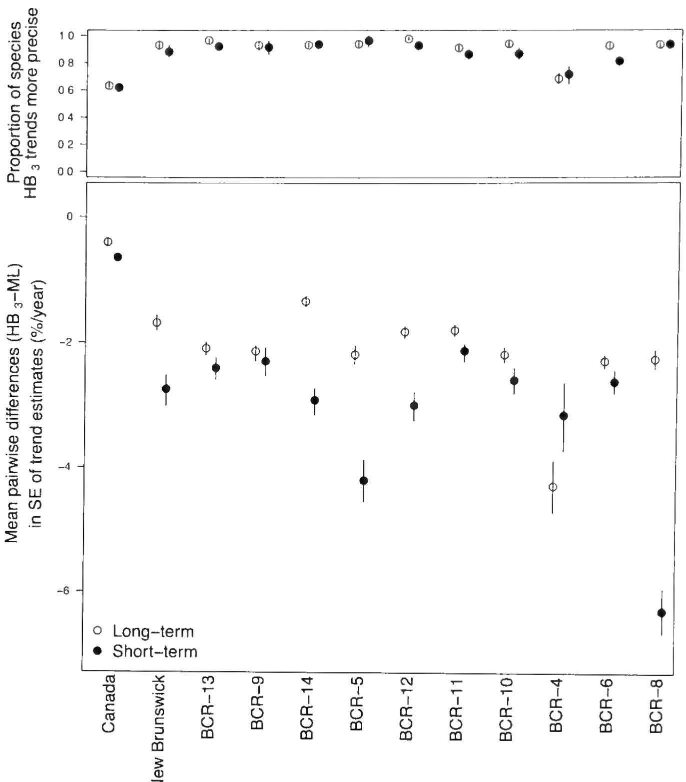

FIGURE 5. Comparisons of precision of Breeding Bird Survey trend estimates between the previously used maximum likelihood (ML) model and the new hierarchical Bayesian model (HB_3) in various regions of Canada. Bird Conservation Regions (BCRs) are arranged in descending order of the ratio of the square root of sample size to area. The upper graph shows the proportion of species in each region for which the HB_3 trend estimates were more precise than the ML trend estimates. The lower graph shows the mean pairwise differences in trend estimates' standard errors (SE); negative values indicate the HB_3 estimates were more precise, i.e., have smaller SEs. Circles and associated error bars represent the means and 95% credible intervals of the posterior distribution of estimates from a trend comparison analysis that accounts for the uncertainty in both the estimates of trend and the estimates of the variance of the trends. See Figure 1 for BCR definitions.

from the ML model were much more variable for species with relatively imprecise annual index estimates (Figure 6B, lower row). For some species, 10-year trends from the HB_3 model were more variable than those from the ML model (points to the left of the diagonal line in Figure 6A); these are species with relatively precise estimates of highly variable annual indices (Figure 6B, upper row).

Scale of annual indices

On average, annual indices from the HB_3 model were somewhat larger than those from the ML model (mean difference = 1.29, 95% credible interval 1.23–1.36), however the log–log relationship closely follows the 1:1 line (Figure 7). Mean estimates from the HB_3 model were more similar to the annual indices from the ML model than those generated by the HB_2 model with a common observer–route effect (mean difference 2.51, 95% credible interval 2.32–2.71). In addition, the differences between the HB_2 and ML model depended on the species' abundance; almost all species with ML indices > 2 were above the 1:1 line and the slope of the

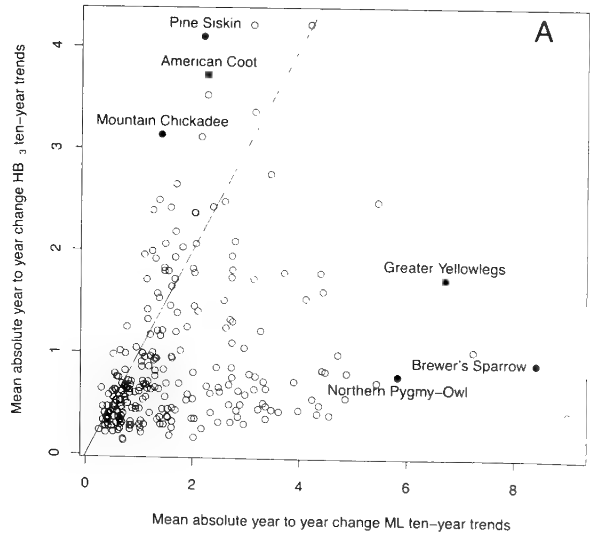

FIGURE 6A.

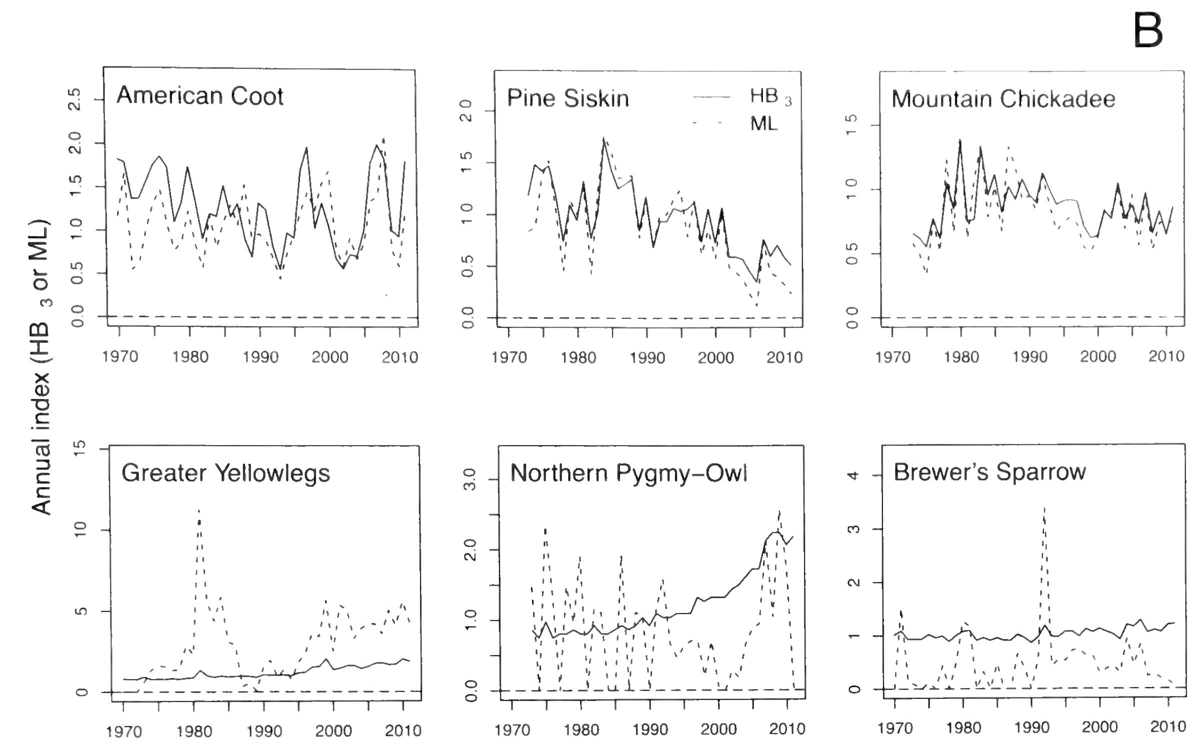

FIGURE 6. Comparison of the year-to-year variability in 10-year Breeding Bird Survey trends for Canada estimated using the maximum likelihood (ML) model and the new hierarchical Bayesian (HB_3) model. A shows the species-level estimates of the absolute year-to-year change in trend values for the two models, from a series of consecutive 10-year trends from $t_{1970\text{-}1980}, t_{1971\text{-}1981}, \ldots, t_{2001\text{-}2011}$. The filled circles indicate the species trends plotted in B. B shows overlays of annual indices from the HB_3 model (solid lines) and the ML model (dashed lines). American Coot (*Fulica americana*), Pine Siskin (*Spinus pinus*) and Mountain Chickadee (*Poecile gambeli*) are examples of species for which the HB_3 trends are more variable, i.e., points above the diagonal in A. Greater Yellowlegs (*Tringa melanoleuca*), Northern Pygmy-Owl (*Glaucidium gnoma*), and Brewer's Sparrow (*Spizella breweri*) are species for which the ML trends are more variable, i.e., points below the diagonal in A.

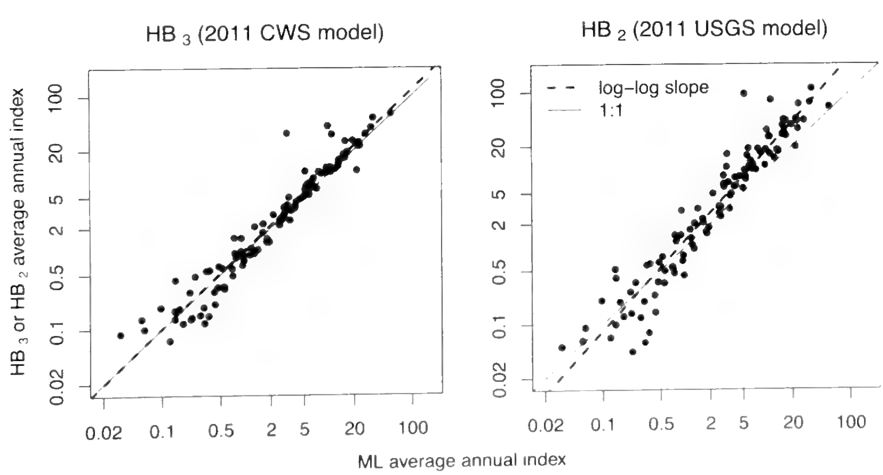

FIGURE 7. Log-scale comparisons of the average of Breeding Bird Survey annual indices for New Brunswick (for 1985–1995) from the previously used maximum likelihood (ML) model, plotted against annual indices from two hierarchical Bayesian models: the new Canadian model (HB_3) and the HB_2 model described in Sauer and Link (2011). Each dot represents one species, and the black dashed lines are predictions from linear models regressing the log of the average annual indices from the two HB models on the log of the average annual indices from the ML model. The solid grey line represents a 1:1 relationship. Note: CWS = Canadian Wildlife Service; USGS = United States Geological Survey

log–log relationship diverged from the 1:1 line (Figure 7).

Discussion

Canadian BBS trends estimated using the HB_3 model are generally similar in magnitude to those estimated from the ML model that was in use between 2002 and 2009. This suggests that for most species, our understanding of population status has not been drastically changed by the adoption of the HB_3 model.

Overall, the trends from the new HB_3 model are more precise, less likely to have extreme values, and less variable among years than those from the previous ML model. A similar hierarchical model (HB_2) showed similar improvements compared with the route-regression model previously used to estimate BBS trends in the United States (Sauer and Link 2011). Although no single model is ideal for all species in all situations, the differences demonstrated here suggest that the HB_3 model provides better information on the population status of approximately 300 bird species breeding in Canada. The broad similarities in trend estimates from the two models are not surprising; the BBS represents a large dataset, and many temporal trends are clear and strong regardless of the analytical models used to estimate them (as noted in similar cross-model comparisons in Thomas and Martin 1996 and Sauer and Link 2011). For some species, the two models generate strikingly different trend estimates, but, in most cases, the estimates are extremely imprecise for both models. For example, in Figure 2, the points that fall far from the 1:1 line are generally very imprecise (i.e., have large credibility ellipses), and the credibility ellipses overlap the 1:1 line in at least one dimension for most of these species.

Magnitude

In some BCRs, long-term trends derived from the HB_3 model are generally more negative/less positive than those from the ML model. This difference is partially the result of a statistical artefact in the ML model; thus, the HB_3 trend estimates are less biased. In the ML model, for years in which a species was not observed in a particular region, the annual index is set to a small arbitrary value. That is, the annual index itself is estimated at zero, but when the trend is calculated, a small constant is added (0.001) so that the log-linear regression can be calculated. For species and regions with these zero counts near either end of a time series, any estimated long-term trend will be strongly influenced by this arbitrary value (O'Hara and Kotze 2010). Because of the smaller number of BBS routes in earlier years, species are more likely to have annual index estimates of zero for those years, and, therefore, their abundance is more likely to be represented by the arbitrary value leading to positive bias in the ML model (Figure 8). In contrast, in the HB_3 model, the annual index for those years is estimated to be a non-zero val-

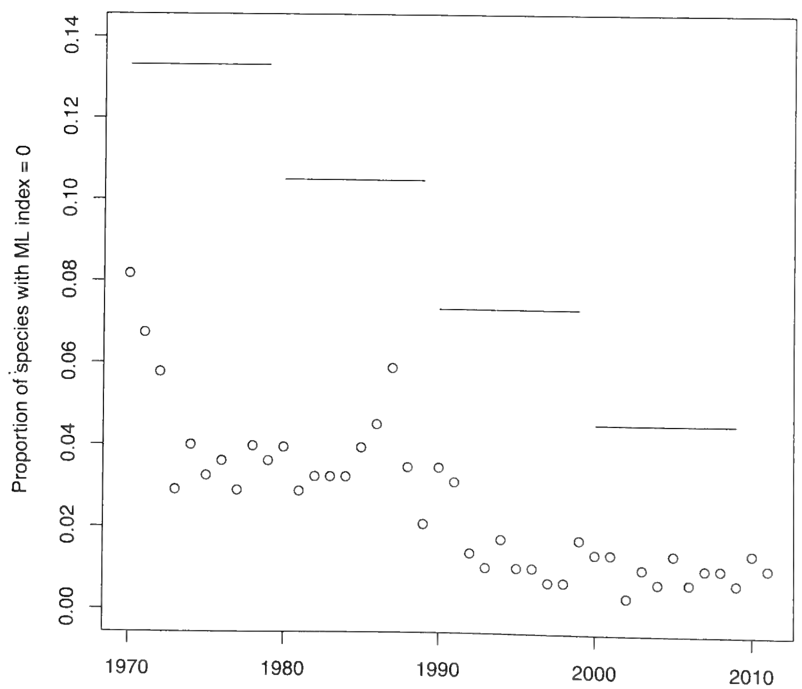

FIGURE 8. Proportion of species with annual index estimates equal to zero when calculated with the maximum likelihood model, previously used to estimate Breeding Bird Survey trends in Canada. Circles indicate annual proportions; horizontal lines indicate proportions of species with at least one annual index equal to zero in each of four decades (1970s, 1980s, 1990s, and 2000s).

ue that reflects the best estimate of the abundance in that year, given the number of routes with zero counts in that year, and the estimates of all other parameters in the model.

Precision

Canadian BBS trends estimated using the HB_3 model were more precise than those from the ML model, and this difference was more pronounced for smaller regions (i.e., New Brunswick and the BCRs). At the national level, the HB_3 model's hierarchical structure makes efficient use of the data and gives moderately more precise estimates than the ML model. For smaller regions, the hierarchical structure of the model results in additional efficiencies. Because the stratum-level parameters are estimated within a single national model, estimates for the error, over-dispersion, first-year observer effects, and the observer–route variance (i.e., the nuisance parameters) share information among strata. This sharing of information makes for more precise stratum-level estimates of the nuisance parameters than would be possible if they were estimated solely from the much smaller set of routes within each stratum. In contrast, the ML model accounts for the observer and route-level nuisance parameters separately within each region.

The HB_3 model's increased precision has important benefits for conservation in that it decreases uncertainty around the assessment of species' status. Steep rates of change or abrupt changes in populations (e.g., 30% decreases in populations that may warrant species at risk status; COSEWIC 2011*) can be identified with greater certainty and over shorter periods of time. Similarly, species can be more confidently classified into status categories, such as those used in Environment Canada's Status of Birds in Canada website (www.ec.gc.ca/soc-sbc).

Variability among years

For most species, the HB_3 short-term trend estimates are less variable among years than the ML short-term trend estimates, because the hierarchical structure of the year-effect parameters makes annual fluctuations much less sensitive to sampling error and annual route coverage. For a few species, short-term HB_3 trend estimates are more variable among years than ML trends, but only when there is relatively strong evidence supporting large annual fluctuations in the population's status. In essence, although short-term HB_3 trend estimates will fluctuate more for populations whose status is well estimated, those fluctuations are likely appropriate because they are more likely to reflect real changes in the populations and not sampling error. In these cases, management decisions that rely on short-term trend estimates, such as COSEWIC status assessments, should also examine the population's recent trajectory to give some context to the trend estimate in any given year. For data-poor populations, the HB_3 model's short-term trends will be more stable across years, so management decisions can be made with some confidence that a species' status assessment will not strongly depend on the year in which it was assessed.

Annual indices

At the stratum level, annual indices from the HB_3 model are very similar to those from the ML model. They are directly interpretable as the expected count by an average observer on an average route in the stratum. They are also more similar in scale to the indices from the ML model than annual indices from the HB_2 model. Estimating observer–route variance at the stratum level in the HB_3 model brings the scaling of the annual indices closer to a scale familiar to users of the ML model results, which is approximately equal to the observed average count across the routes run in any given year.

The improvement in scaling of the annual indices in the HB_3 model over the HB_2 model also has an influence on regional trends, because it better reflects the variation in abundance among strata. Because regional annual indices are sums of the stratum-level indices, the relative contribution of each stratum's trend to a regional trend is partly mediated by the relative abundance of birds in each stratum. In relatively rare but potentially important cases, regional trends from the HB_3 and HB_2 models can be strikingly different: where the average abundance, trend, and observer–route variance are highly variable among strata. For example, the HB_2 model applied to Canadian data for Wood Thrush (*Hylocichla mustelina*) estimates the national trend at −1.8 (95% credible interval −2.6 to −0.9), while the HB_3 model estimates the national trend at −4.4 (95% credible interval −5.3 to −3.6). This large difference — the credible intervals do not overlap — is due to the relative weight in the two analyses of the largely stable Wood Thrush population in southern Ontario (Ontario BCR 13). In this region, the observer–route variance is much lower than in any other stratum in the analysis. As a result, the observer–route variance retransformation factors are very different in the two models ($\sigma^2_{\omega} >> \sigma^2_{\omega BCR13}$). The larger retransformation factor in the HB_2 model creates annual indices that overestimate the observed abundance of Wood Thrush in southern Ontario by a factor of 3 and, similarly, overestimate the proportion of the national population that occurs in the region and, therefore, its influence on the national trend.

Users of published BBS estimates should be aware that the scale of annual indices from the HB_3 model and the ML model may differ because the models account differently for routes in regions not included in each species analysis. The HB_3 model estimates an annual index scaled to the expected count averaged across routes within the strata included in the analysis, i.e., it excludes routes where the species data are too sparse or that are outside the species' breeding range. The ML model's annual indices are scaled to the expected count averaged across all routes within the re-

gion being analyzed, e.g., for national trends, all routes run in the country are included, regardless of whether they fall within the species' breeding range. For broadly distributed and common species, for which all strata and all routes are included in the HB_3 analysis, the scales of the national estimates from each model will be equal. For more locally distributed species, for which the HB_3 analysis only includes a subset of the strata (e.g., any species that breeds exclusively west of the Rockies), the HB_3 annual indices will be scaled to a much higher abundance because they ignore all of the routes and strata outside of the species' breeding range, where the average counts are zero. It is important to note that this difference does not affect our quantitative comparisons of annual indices among the HB_3, ML, and HB_2 models (i.e., Figure 7), because we compared them within a single stratum, nor does it affect trend estimates in the two models; it only affects the scale of the annual indices.

Improved population inference from BBS

Beyond the quantitative comparisons, some philosophical arguments suggest that the HB_3 model represents an improvement over the ML model. First, the Bayesian framework provides much more intuitive and flexible inference than the frequentist framework of the ML model. The correct inferential interpretation of Bayesian credible intervals is almost certainly a more natural expression of the type of inference that users of BBS trends desire, i.e., there is a 95% probability that the trend is greater than the lower bound and less than the upper bound. In contrast, the correct interpretation from frequentist analyses (usually confined to tests of significance) do not relate to the estimates of population change, but to the data that were sampled, e.g., if the true rate of population change is zero, there is less than a 5% chance of observing the data that were collected. In addition, the ability to estimate the full posterior distribution of a broad suite of derived parameters, such as the probability that the population has declined more than 50% in 10 years (i.e., one of the COSEWIC criteria for "Endangered" status), provides a practical and flexible approach to assessing the uncertainty around particular conclusions one might draw from a BBS trend.

Second, the HB framework and the HB_3 model in particular provide an efficient, flexible, coherent and complete framework for the analysis, which the ML model lacks. The hierarchical structure of the model makes efficient use of the data and is less sensitive to annual variation in sampling error. In addition, the HB_3 model can be expanded easily to include covariables and explicit spatial structure (e.g., Thogmartin *et al.* 2004; Nielson *et al.* 2008), and the HB framework lends itself well to composite and comparative analyses of the BBS and other surveys (e.g., Link and Sauer 2007 and the method used here to compare the magnitude and precision of trends from the two models). Finally, the HB_3 model estimates trends and annual indices within a single coherent model structure which the ML model lacks. For example, the ML model requires the addition of an arbitrarily chosen constant to some years' annual indices to estimate trends.

A third example of improved inference from results of the HB_3 model is that the trends and estimates of uncertainty around trends for multi-strata regions (e.g., national trends), are a much clearer reflection of the full uncertainty of the population status estimates within the region. That is, regional and national estimates are combinations of stratum-level estimates, appropriately weighted by the proportion of the species' breeding population in each stratum (by summing indices of relative abundance, weighted by the stratum's area). In addition, the strata in the HB_3 model are more likely to reflect spatial variation in population trends and trajectories than the degree-block strata in the ML analysis. The HB_3 strata are structured on BCRs, which are relevant to population processes, and political units, which are relevant to management and human activity. In contrast, inferences regarding trends and uncertainty from the ML model only apply to the degree blocks included in the analysis, i.e., degree-blocks with data. Furthermore, the degree-block weighting of the ML model means that the relative influence of populations with potentially disparate trends and trajectories among different regions (i.e., BCRs and political units) depends on the relative sampling intensity of the BBS in those regions (i.e., the number of degree-blocks with data). For example, the White-throated Sparrow (*Zonotrichia albicollis*) occurs on BBS routes in the southern BCRs (12, 13, and 14), where there are many degree-blocks with data and where trends are strongly negative. However, the bulk of its population occurs in the more northern BCRs (6, 7, and 8), where trends are relatively stable and there are few degree-blocks with data. The degree-block weighting of the ML analysis puts relatively more weight on the decreasing southern populations (national short-term ML trend −0.9%/year [95% confidence interval −1.7% to −0.1%]), whereas the stratum area weights of the HB_3 analysis put more weight on the more positive and much less precisely estimated trends from the northern populations (national short-term HB_3 trend 0.59%/year [95% credible interval −1.64% to 3.87%]). The estimated average trend from the HB_3 model better reflects the status of the bulk of the Canadian population of the White-throated Sparrow in the northern BCRs and, given that the northern BCRs are relatively poorly surveyed by the BBS, the wider credible interval of the national HB_3 trend is a more appropriate measure of the uncertainty around the population's status. This more appropriate weighting of imprecisely measured trends from regions that are relatively large but poorly surveyed also explains the modest improvements in precision at the national level, relative to the greater improvements within individual BCRs (Figure 3).

Because of the flexibility of the HB_3 model framework, the best short-term trend and the best long-term trend do not necessarily include data from the same spatial areas. Since 1966, spatial coverage by Canadian BBS routes has expanded gradually into the more northerly strata. The earliest BBS routes in Canada were run in the Maritimes and Quebec in 1966. By the early 1970s, much of southern Canada had adequate coverage. However, some more northerly regions have only had adequate coverage for the last 20 years. Because of the paucity of data from the Northwest Territories and much of the Yukon before the late 1980s or later, trends in these areas cannot reasonably be extrapolated back to 1970. Long-term trend estimates for large regions (e.g., national trends) can be estimated, but they must exclude some strata, for which we have only recent data. In contrast, short-term estimates for those regions should include all of the strata with data. In the HB_3 model, deriving separate short- and long-term trend estimates that include different strata is a straightforward process of summarizing stratum-level annual estimates, and it retains the entire posterior distribution of all derived estimates. To get similar separate trends from the ML model would require multiple runs using different subsets of the data, and each subset would have a reduced sample size and, therefore, reduced precision.

Limitations of the HB_3 model and future evolution

Along with the benefits of a complex hierarchical model structure come complex consequences for population inference. For example, the trend term in the HB_3 model combined with the distributional assumptions of the random year-effects terms means that, for years with relatively sparse or highly variable data, annual indices will tend to track a fitted estimate of the species' long-term trend. These assumptions and model structure are reasonable, given that the long-term trend is estimated from the data. However, in some cases, they could lead to an over-smoothing of the annual indices. For example, the model does not account for autocorrelation in the sequence of successive year-effects and could, therefore, be insensitive to cyclical population patterns, unless each individual year contained relatively strong evidence of a departure from the long-term trend. Similarly, the number of BBS routes in Canada has more than doubled since 1980, and, therefore, sparser data in the early years means that those early annual indices are less likely to depart from the long-term trend than annual indices in later years. Although these assumptions greatly reduce the influence of sampling errors on trend estimates (Link and Sauer 2002), as evidenced by the reduced inter-annual variability of HB_3 trend estimates (Figure 6), there are species for which the smoothing of annual indices could lead to bias in both the individual indices and the trends. Future refinements of the model may include terms to model the temporal autocorrelation in the year-effects, so that the model will more closely reflect population fluctuations when successive years show similar departures from the long-term trend.

Conclusion

Overall, the use of the HB_3 model to estimate trends and annual indices of abundance provides improved information on the population status of birds in Canada. Estimates from the HB_3 model are generally similar in direction and magnitude to estimates from the previous model, but they offer greater precision, less variation among years, a better representation of the spatial variation in population status across Canada, and a more intuitive and flexible assessment of uncertainty. As statistical science evolves, the analysis of BBS data will follow suit, continuing to improve as it has in the past. This evolution and improvement honours the contributions of the thousands of volunteers who have participated in the BBS since its inception, and ensures that this survey will remain at the forefront of our understanding of the status of Canada's and North America's birds.

Acknowledgements

We thank the thousands of skilled volunteers who have contributed to the Breeding Bird Survey over the years, as well as those who have served as provincial and territorial coordinators. Our thanks also go to Pete Blancher, Brian Collins, Bill Link, David A. W. Miller, John Sauer, and Joe Veech for their insightful comments and review of the paper, model development or both.

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Supplementary material available at:
http://www.canadianfieldnaturalist.ca

Received 23 September 2013
Accepted 22 November 2013

SUPPLEMENTARY MATERIAL:

APPENDIX 1. Detailed description of the maximum likelihood (ML) model used to generate Canadian Breeding Bird Survey trends before 2010.

APPENDIX 2. WinBUGS (Bayesian inference Using Gibbs Sampling) language descriptions of the hierarchical Bayesian models.

APPENDIX 3. Microsoft Excel workbook showing differences in trend estimates between the maximum likelihood (ML) and the hierarchical Bayesian (HB_3) models, with separate worksheets for short- and long-term trends and for each Bird Conservation Region, Canada, and New Brunswick.

APPENDIX 4. Additional comparisons of the hierarchical Bayesian (HB_3) and maximum likelihood (ML) models, including comparisons of the number of species with trend estimates and the classification of species trends into the categorical assessments of population status used in Environment Canada's Status of Birds in Canada website (Environment Canada 2011).

Acoustic Monitoring of Migratory Birds over Western Lake Erie: Avian Responses to Barriers and the Importance of Islands

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Sanders, Claire E., and Daniel J. Mennill. 2014. Acoustic monitoring of migratory birds over western Lake Erie: avian responses to barriers and the importance of islands. Canadian Field-Naturalist 128(2): 135–144.

Understanding the flight patterns of migrating birds is critical for informing conservation actions and management decisions. We studied the geographic and temporal distribution of birds migrating through the southern Great Lakes using nocturnal acoustic monitoring data and banding records from sites on Pelee Island in Lake Erie and on the mainland along the north shore of Lake Erie. Given that Lake Erie may represent an ecological barrier to migratory birds, we predicted that mainland and island sites would show different patterns in both the number of passage migrants and the timing of their migration. Analysis of over 60 000 flight calls from 6200 h of recordings revealed significantly more migrants over the island than the mainland in both spring and fall 2012. The acoustic data provide evidence that none of the species or species groups examined avoided crossing the lake. Birds were detected significantly earlier on Pelee Island than on the north shore of Lake Erie in spring, although they were not detected earlier on the mainland in fall. These results suggest that Lake Erie is not a major barrier to migration. The large number of birds detected over the island suggest that birds may concentrate their flight over islands in the middle of the lake, although recordings of migrants over open water will be required to support this suggestion. Our results show that Pelee Island is an important part of the migratory route of North American birds and provide valuable information on the movement of nocturnal migrants over the Great Lakes.

Key Words: acoustic monitoring; banding; bird migration; ecological barriers; geographic barriers; night-flight calls; Lake Erie; Essex County; Ontario; Pelee Island

Introduction

Migratory birds can fly non-stop for thousands of kilometres (Egevang *et al.* 2010; Bairlein *et al.* 2012; Battley *et al.* 2012) and are likely to encounter ecological barriers, such as bodies of water, mountain ranges, or stretches of desert as they move between breeding and wintering grounds. Numerous factors might lead birds to select circuitous routes rather than cross over ecological barriers (Alerstam 2001), including their own body condition and external information such as weather conditions (Schmaljohann and Naef-Daenzer 2011). The increased risk of crossing an ecological barrier may be offset by the time or energy saved in using the shortest migratory route (Bruderer 2001). This may be particularly important during spring migration, when urgency drives males to reach their breeding grounds to compete for prime territory and attract mates (Francis and Cooke 1986).

Migration strategies and the behaviour of migrating birds are well-studied areas of ornithology (Moore and Kerlinger 1987; Gauthreaux and Belser 1999). During a journey from Africa to Europe, for example, migratory birds encounter the Sahara Desert, the Mediterranean Sea, and the Alps, all of which could pose a threat to the long-distance migrant. Historically, researchers believed that birds were distributed homogenously as they navigated the Mediterranean (Bruderer 2001); however, banding studies have demonstrated that birds exhibit diverse migration strategies when encountering ecological barriers (Spina and Pilastro 1999). In the Mediterranean, radar studies have shown that the number of migrants over water is often a third to half that over the Iberian Peninsula, demonstrating that most birds prefer to circumnavigate the sea (Bruderer and Liechti 1999). Furthermore, islands and peninsulas appear to play an important role for migrants that choose to cross the Mediterranean Sea, although the use of island stopovers varies among species and within species based on age and sex (Barriocanal and Robson 2007).

The Gulf of Mexico is a major ecological barrier in North America. Birds vary in their propensity to cross the water of this gulf (Stutchbury *et al.* 2009). For example, geolocator data from a Wood Thrush (*Hylocicha mustelina*) suggest that it crossed the Gulf of Mexico during its northward migration, but went around on its southward journey; another thrush chose a land-based route on its northward spring migration but then crossed the gulf in the two subsequent spring migrations (Stanley *et al.* 2012). Barrier islands along the Mississippi coast play an important role for some migrants, providing habitat for foraging before or after the substantial journey across the gulf (Moore *et al.* 1990).

North America's Great Lakes are ecological obstacles that influence the migration of songbirds (Diehl *et al.* 2003; Deutschlander and Muheim 2009). The geography of the lakes channels millions of spring and fall migrants through the region. The north and south shores of Lake Erie, as well as the Lake Erie island archipelago, are important stopover locations, and many parts of this region have been designated Important Bird

Areas by Bird Studies Canada and Nature Canada because of their seasonal concentration of migratory birds (BirdLife International n.d.*). However, because of the technical challenges involved in monitoring nocturnal migration of many bird species, we lack significant information on the ecology and behaviour of migratory birds that pass through the Great Lakes. Recent radar studies in the region have explored ecological barrier avoidance (Diehl *et al.* 2003), as well as habitat use by migrant birds and stopover ecology (Bonter *et al.* 2009). Radar data confirm that many migrants cross the Great Lakes in spring and fall, although higher densities of birds were always detected over land than over water during migration (Diehl *et al.* 2003). Little is known about the importance of the islands in western Lake Erie to migratory bird species.

Although general patterns of barrier avoidance can be revealed through radar studies of migratory birds, it is not possible to distinguish between bird species using radar. In addition, if nocturnal migrants travel at lower altitudes than diurnal migrants, as reported in the Gulf of Mexico, they may not be detected by radar (Farnsworth and Russell 2005). Acoustic monitoring technology overcomes these limitations. Using species-specific signatures of the flight calls of migratory birds, we can collect detailed population and behavioural information on cryptic, aquatic, and nocturnal species that are otherwise difficult to monitor (Marques *et al.* 2013). We recently showed that night-flight call data can be used to determine the timing and magnitude of spring and fall migration through the southern Great Lakes (Sanders and Mennill *in press*). Therefore, night-flight call data may improve our understanding of the spatial and temporal distribution of avian migration patterns in the western basin of Lake Erie.

In this investigation, we used night-flight call data and banding station records to determine whether Lake Erie acts as an ecological barrier to migratory birds by comparing the number of birds detected on an island mid-way across the lake versus the number detected on the north shore. If Lake Erie acts as an ecological barrier, we expected to find a smaller community of migrants over the island than on the mainland. If Lake Erie does not serve as an ecological barrier, but instead concentrates birds over the island chain as they cross the lake, then we expected to detect more migratory birds over the island than at mainland sites. Finally, if Lake Erie does not serve as a barrier, but an obstacle that temporarily delays the migration of birds, we expected to see a lag in detection between the southerly island and the northerly mainland sites in spring migration, and the reverse pattern in the fall.

Study Area

We studied bird migration in Essex County, Ontario, during the 2012 spring migration from April 15 to June 15 and the 2012 fall migration from August 15 to November 10. We recorded night-flight calls at seven locations (Figure 1). Three recording sites were located on Pelee Island mid-way across Lake Erie: two at a bird banding station in Fish Point Provincial Nature Reserve at the southern end of the island (41°44'N, 82°40'W) and one 15 km north at Lighthouse Point Provincial Nature Reserve at the northern end of the island (41°47'N, 82°38'W). Four recording sites were located on the north shore of Lake Erie: Holiday Beach Migration Observatory in the Holiday Beach Conservation Area (42°02'N, 83°02'W); a private woodlot near McGregor, Ontario (42°06'N, 82°59'W); Cedar Creek Conservation Area (41°00'N, 82°47'W); and Point Pelee National Park (41°56'N, 82°30'W).

Methods

Acoustic recordings

At each of the seven recording sites, we deployed an autonomous digital recorder (SM-2 Song Meter, Wildlife Acoustics, Concord, Massachusetts) equipped with a single night-flight call microphone (SMX-NFC, Wildlife Acoustics), mounted on a 30 × 30 cm plastic plate to minimize recording of sounds below the microphone. We attached the microphone to a 5.8-m pole that we lashed to a tree or post at the seven recording sites. To minimize interference noise from leaves, insects, and amphibians, we positioned the microphones just above tree height. With seven identical microphones all mounted in similar fashion above the trees, we assumed that each of our seven recorders was equally capable of detecting the night-flight calls of birds passing overhead.

As recommended in eBird's Nocturnal Flight Call Count Protocol (eBird n.d.*), we programmed recorders to begin sampling at astronomical dusk and conclude at astronomical dawn (approximately 70 minutes after sunset to 70 minutes before sunrise), when the sun was more than 18° below the horizon. Recordings were collected at 44 100-Hz sampling frequency with 16-bit accuracy in WAVE format in 1-h and 59-minute files (1-minute silent intervals between files allowed the recorders to write the recordings to memory cards). Each recorder was visited every 3–5 days to change batteries and collect recordings.

Recordings were processed manually to ensure the greatest possible accuracy in detecting all flight calls, as recommended by Swiston and Mennill (2009). We processed recordings in two stages (for detailed description see Sanders and Mennill *in press*). Briefly, recordings were first visualized as sound spectrograms using Syrinx-PC sound analysis software (J. Burt, Seattle, Washington) and scanned 30 s at a time, by a team of 12 volunteer sound analysts (spectral settings: 1024 FFT size, Blackman window). We used the time and frequency cursors in Syrinx-PC to annotate all night-flight calls in our recordings.

During the second stage of processing, we classified the species or species group of as many night flight calls as possible. Using both time and frequency characteristics of the spectrograms of various flight calls

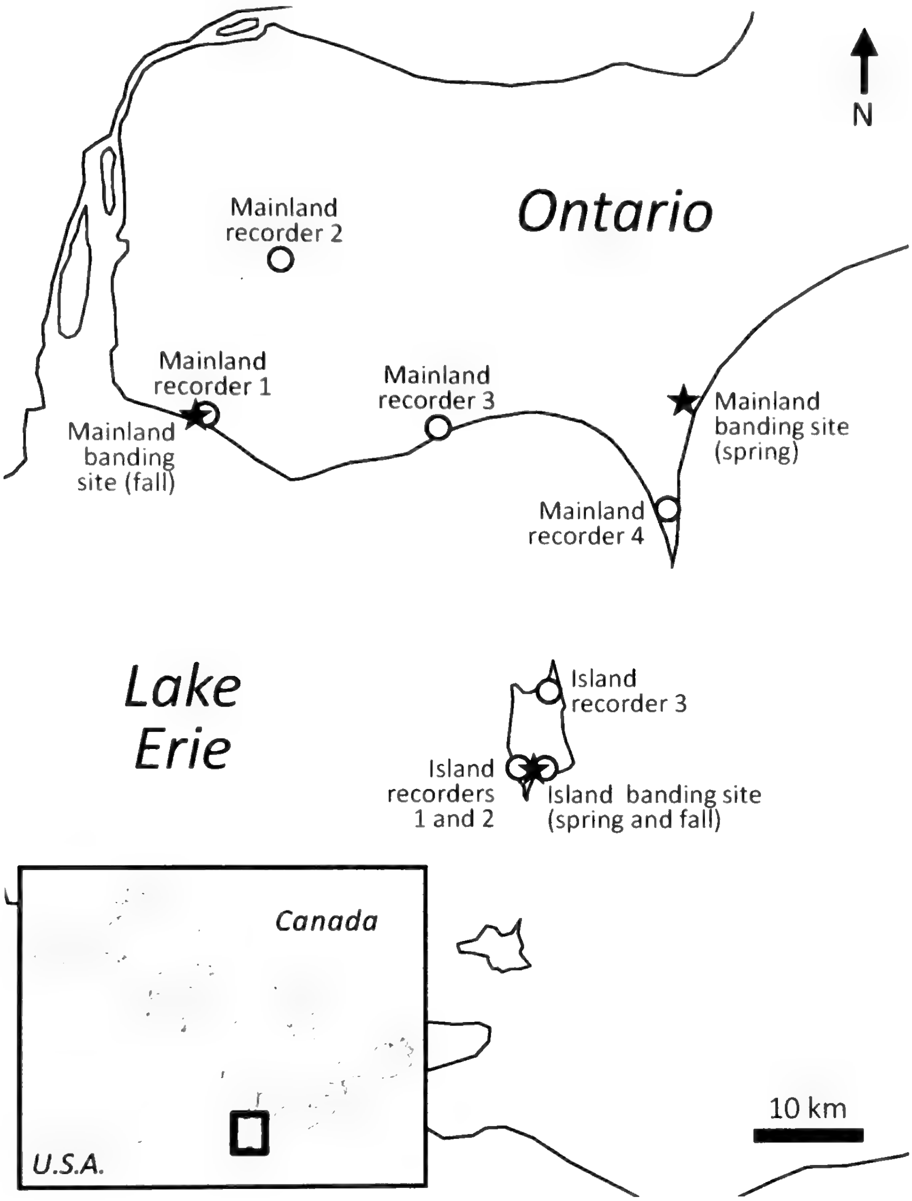

FIGURE 1. Map of study area showing the seven acoustic recording locations (white circles) and the three banding stations (black stars) used to study spring and fall migration in 2012 around the western basin of Lake Erie, Essex County, Ontario.

to distinguish between species (Sanders and Mennill *in press*, Appendix 1), we constructed a classification chart modified from Evans and Rosenberg (2000). After evaluating our own recorded flight calls and reference recordings (Evans and O'Brien 2002*), we determined that 67 species of nocturnal migrants could be identified to the species level (i.e., their night-flight calls were distinctive) or into seven bioacoustic categories, or species groups, each comprising multiple bird species whose calls could not be distinguished from one another (details in Sanders and Mennill *in press*, Appendix 1). For example, the night-flight calls of Northern Parula (*Setophaga americana*) and Pine Warbler (*S. pinus*) both appear as a single down-sweep on a sound spectrogram; thus, we pooled the detections for these species into the "single down-sweep" species-group category (Sanders and Mennill *in press*, Appendix 1). Furthermore, several species spanned multiple bioacoustic categories or were classified as distinct at the species level as well as a member of a broader category. For example, Ovenbirds (*Seiurus aurocapilla*) produce a distinctive checkmark-shaped flight call that is species-specific, but also produce calls that consist only of a frequency modulated upsweep (i.e. the "up" complex; Sanders and Mennill *in press*).

Banding data

Banding data were collected at two migration monitoring stations that operated mist nets concurrent with

our recordings. During spring 2012, birds were banded at Fish Point Provincial Nature Reserve on Pelee Island and at Hillman Marsh Conservation Area on the north shore of Lake Erie from April 15 to June 10. During fall 2012, birds were banded at Fish Point Provincial Nature Reserve on Pelee Island and at Holiday Beach Conservation Area on the north shore of Lake Erie from August 15 to November 10.

The type of species captured in mist nets is heavily influenced by local habitat; the nets at both Pelee Island and Holiday Beach banding stations are located in similar habitats of semi-mature deciduous forest dominated by Silver Maple (*Acer saccharinum*) and Red Maple (*Acer rubrum*), with Eastern Cottonwood (*Populus deltoides*), Black Ash (*Fraxinus nigra*), American Elm (*Ulmus americana*), Common Hackberry (*Celtis occidentalis*), and Pin Oak (*Quercus palustris*). The Hillman Marsh banding station operates in an early successional habitat previously dominated by hawthorn (*Crataegus* sp.), Rough-leaved Dogwood (*Cornus drummondii*), Eastern White Pine (*Pinus strobus*), Black Cherry (*Prunus serotina*), Northern Red Oak (*Quercus rubra*), willow shrubs (*Salix* sp.), and some Pin Oak (*Quercus palustris*). The banding station on Pelee Island used 10 mist nets and followed the monitoring protocol recommendations of Hussell and Ralph (2005). The nets at this station were open half an hour before sunrise and ran for 6 h, excluding down time when nets were closed due to bad weather (rain or wind) or high bird volume when nets were closed to ensure safe and efficient bird handling. The Holiday Beach Migration Observatory operated both the banding stations on the mainland at Hillman Marsh and Holiday Beach. As a volunteer organization, this observatory's research efforts varied with the availability of volunteers; seven nets were in use at Hillman Marsh in spring 2012 and 16 at Holiday Beach in fall.

To facilitate comparisons with our acoustic data, we pooled banding records for the species that made up each of our acoustic species groups (e.g. given their similar night-flight calls, we pooled together all Fox Sparrows and Song Sparrows captured in mist nets in a "FOSP/SOSP" species group of bird captures).

Statistical analysis and sample size

To determine whether there were more detections over the island or the mainland, we combined the detections from all mainland recorders, adjusted for the number of hours per recorder, and calculated the average number of calls per recording station. We repeated this process for the island recorders to produce a relative number of calls per recording station for each species or species group (Table 1). We used sign tests to determine whether the number of acoustic detections over the island was less than the number over the mainland across 38 species and species groups. Given the well-established problems of estimating abundance from mist net records (Karr 1981) — especially due to the strong influence of surrounding habitat — we did not compare the total number of birds in mainland and island mist nets.

TABLE 1. Number of classified acoustic detections (per 1000 h of recording) and mist net detections (per 1000 h of netting) of migratory birds in spring and fall 2012 at mainland and island locations in Essex County, Ontario.

Bioacoustic		Spring migration				Fall migration			
		Acoustic detections		Net detections		Acoustic detections		Net detections	
category	Species or species group ($n = 38$)	Mainland	Island	Mainland	Island	Mainland	Island	Mainland	Island
Zeep	Bay-breasted Warbler (*Dendroica castanea*)	75.49	228.44	62.11	82.07	834.49	1236.09	64.64	54.32
	Blackburnian Warbler (*Dendroica fusca*)								
	Blackpoll Warbler (*Dendroica striata*)								
	Cerulean Warbler (*Dendroica cerulea*)								
	Connecticut Warbler (*Oporornis agilis*)								
	Louisiana Waterthrush (*Seiurus motacilla*)								
	Magnolia Warbler (*Dendroica magnolia*)								
	Worm-eating Warbler (*Helmitheros vermivorum*)								
	Yellow Warbler (*Dendroica petechia*)								
Up	Black-throated Green Warbler (*Dendroica virens*)	741.08	2275.02	86.23	145.31	1113.25	1637.27	28.27	148.76
	Mourning Warbler (*Oporornis philadelphia*)								
	Nashville Warbler (*Vermivora ruficapilla*)								
	Orange-crowned Warbler (*Vermivora celata*)								
	Ovenbird (*Seiurus aurocapilla*)								

TABLE 1. (continued) Number of classified acoustic detections (per 1000 h of recording) and mist net detections (per 1000 h of netting) of migratory birds in spring and fall 2012 at mainland and island locations in Essex County, Ontario.

		Spring migration				Fall migration			
		Acoustic detections		Net detections		Acoustic detections		Net detections	
Bioacoustic category	Species or species group (n = 38)	Mainland	Island	Mainland	Island	Mainland	Island	Mainland	Island
	Tennessee Warbler (*Vermivora peregrina*) Vesper Sparrow (*Pooecetes gramineus*) White-crowned Sparrow (*Zonotrichia leucophrys*) Yellow-rumped Warbler (*Dendroica coronata*)								
Single down-sweep	Northern Parula (*Parula americana*) Pine Warbler (*Dendroica pinus*)	73.18	236.74	0.73	0.67	106.60	157.56	1.32	0.36
Double down-sweep	Field Sparrow (*Spizella pusilla*) Savannah Sparrow (*Passerculus sandwichensis*)	281.18	738.26	2.92	0	856.79	1117.48	0.17	0
FOSP/SOSP	Fox Sparrow (*Passerella iliaca*) Song Sparrow (*Melospiza melodia*)	95.52	524.36	8.77	0	180.19	381.99	2.48	7.1
LISP/SWSP	Lincoln's Sparrow (*Melospiza lincolnii*) Swamp Sparrow (*Melospiza georgiana*)	10.01	47.76	59.19	14.13	15.61	40.12	1.16	2.49
Cuckoo	Black-billed Cuckoo (*Coccyzus erythropthalmus*), Yellow-billed Cuckoo (*Coccyzus americanus*)	16.18	46.73	0	0.67	0.00	0.00	0.33	0
AMRE	American Redstart (*Setophaga ruticilla*)	53.92	169.25	10.23	10.09	64.23	166.28	21.16	35.5
AMRO	American Robin (*Turdus migratorius*)	15.41	16.61	13.88	8.07	0	0.58	1.32	1.07
ATSP	American Tree Sparrow (*Spizella arborea*)	1.54	12.46	0	0	74.04	104.65	0.5	0.71
BAWW	Black-and-white Warbler (*Mniotilta varia*)	5.39	15.58	7.31	11.44	3.12	7.56	9.59	10.65
BOBO	Bobolink (*Dolichonyx oryzivorus*)	10.78	31.15	0	0	7.14	8.72	0	0
BTBW	Black-throated Blue Warbler (*Dendroica caerulescens*)	10.01	18.69	2.19	6.05	22.75	45.35	16.7	29.11
CAWA	Canada Warbler (*Wilsonia canadensis*)	2.31	17.65	5.12	14.8	0.89	2.91	2.81	2.84
CMWA	Cape May Warbler (*Dendroica tigrina*)	7.70	15.58	0.73	0.67	18.29	37.79	2.48	1.07
COYE	Common Yellowthroat (*Geothlypis trichas*)	19.26	51.92	54.8	18.84	22.30	57.56	1.65	2.13
CSWA	Chestnut-sided Warbler (*Dendroica pensylvanica*)	11.56	67.49	8.04	13.45	29.88	67.44	4.96	3.91
CHSP	Chipping Sparrow (*Spizella passerina*)	451.43	726.84	0	0	210.96	345.36	0	0
DEJU	Dark-eyed Junco (*Junco hyemalis*)	11.56	14.54	0	0	17.84	51.16	2.81	11.36
GCKI	Golden-crowned Kinglet (*Regulus satrapa*)	0	0	0	0	33.90	64.54	52.57	109.35
GCTH	Grey-cheeked Thrush (*Catharus minimus*)	30.04	52.96	9.5	10.76	132.91	138.38	6.45	61.07
GRSP	Grasshopper Sparrow (*Ammodramus savannarum*)	5.39	32.19	0	0	0.45	0.58	0	0
HETH	Hermit Thrush (*Catharus guttatus*)	55.47	125.64	18.27	18.16	18.29	45.35	10.91	60.36
HOWA	Hooded Warbler (*Wilsonia citrina*)	2.31	3.12	0	1.35	0.45	1.74	0	0
INBU	Indigo Bunting (*Passerina cyanea*)	23.11	63.34	7.31	6.05	15.61	42.44	0.33	1.07
NOWA	Northern Waterthrush (*Seiurus noveboracensis*)	7.70	21.81	7.31	6.05	9.37	19.19	1.16	5.33
OVEN	Ovenbird (*Seiurus aurocapilla*)	50.07	165.10	10.23	21.53	41.48	59.89	4.96	24.14

TABLE 1. (continued) Number of classified acoustic detections (per 1000 h of recording) and mist net detections (per 1000 h of netting) of migratory birds in spring and fall 2012 at mainland and island locations in Essex County, Ontario.

Bioacoustic		Spring migration				Fall migration			
		Acoustic detections		Net detections		Acoustic detections		Net detections	
category	Species or species group (n = 38)	Mainland	Island	Mainland	Island	Mainland	Island	Mainland	Island
PAWA	Palm Warbler (*Dendroica palmarum*)	30.04	138.10	5.12	12.78	34.34	104.07	0.17	0
PISI	Pine Siskin (*Carduelis pinus*)	0	0	0	0	7.58	5.81	0	0
RBGR	Rose-breasted Grosbeak (*Pheucticus ludovicianus*)	20.80	31.15	0.73	4.04	3.12	11.05	0	0.36
SCTA	Scarlet Tanager (*Piranga olivacea*)	6.16	10.38	0	0	1.78	0.58	0	0
SWTH	Swainson's Thrush (*Catharus ustulatus*)	905.17	1936.52	9.5	19.51	921.46	2430.32	28.93	199.89
VEER	Veery (*Catharus fuscescens*)	167.94	363.42	11.69	7.4	38.80	78.49	2.31	21.66
VESP	Vesper Sparrow (*Pooecetes gramineus*)	6.93	3.12	0	0	4.46	17.44	0	0
VIRA	Virginia Rail (*Rallus limicola*)	2.31	16.61	0	0	0.45	0	0	0
WIWA	Wilson's Warbler (*Wilsonia pusilla*)	2.31	2.08	4.38	5.38	9.37	14.54	6.11	0.71
WOTH	Wood Thrush (*Hylocichla mustelina*)	32.35	75.80	2.92	5.38	0	2.33	0.17	1.42
WCSP	White-crowned Sparrow (Zonotrichia leucophrys)	73.95	148.48	0	2.02	84.30	120.93	0	0
WTSP	White-throated Sparrow (*Zonotrichia albicollis*)	445.27	2727.74	84.03	24.22	511.58	1793.67	11.9	45.8

To determine whether some species were present at the mainland sites, but not the island sites, we examined both the acoustic and banding data for the presence or absence of each species or species group in both spring and fall.

To determine whether the date of first detection on the island was different from that on the mainland, we used Wilcoxon sign-rank tests to compare average arrival dates for all species. We pooled the data for the four mainland recorders and calculated the average first detection date for all species or species groups at the mainland sites, and repeated this process for island recorders and sites. We performed a parallel analysis using banding data to compare first arrival dates at the island and mainland banding stations in spring and fall.

Results

We collected 2261 h of recordings over 58 nights at the seven recording locations during the spring migration and 3960 h of recordings over 63 nights at the same locations during the fall migration, for a total of 6237 h of recordings over both seasons. In these recordings, we noted 60 013 nocturnal flight calls: 22 554 during spring migration and 37 567 during fall migration. We were able to classify, with confidence, 46 846 (78%) calls to species or species group: 16 646 (74%) spring recordings and 30 200 (81%) fall recordings. There was substantial variation in the number of night-flight call detections at the various recording locations in spring and fall (Table 2).

During the spring migration, 834 birds were banded at the island site and 910 birds were banded at the mainland site. During the fall migration, 2079 birds were banded at the island site and 2711 birds were banded at the mainland site.

Number of migrants detected on mainland versus island

During spring migration, we detected more night-flight calls on the island than on the mainland (Table 1): 35 species or species groups were more abundant on the island; only two species — Vesper Sparrow (*Pooecetes gramineus*) and Wilson's Warbler (*Wilsonia pusilla*) — were more abundant on the mainland (sign test, $P < 0.0001$, $n = 37$); two of the species indicated in Table 1 were not detected on either the mainland or island recorders in spring: Golden-crowned Kinglet (*Regulus satrapa*) and Pine Siskin (*Carduelis pinus*).

Similarly, during fall migration, we also detected more calls on the island than on the mainland (Table 1): 35 species or species groups were more abundant on the island; only three species — Pine Siskin, Scarlet Tanager (*Piranga olivacea*), and Virginia Rail (*Rallus limicola*) — were more abundant on the mainland (sign test, $P < 0.0001$, $n = 38$; cuckoos were not detected by either mainland or island recorders in fall).

Species detected on mainland versus island

Acoustic monitoring data revealed that the same composition of species passed over the mainland and

TABLE 2. Total number of acoustic detections (including both classified and unclassified detections) per 1000 h recording time during spring and fall migration, 2012, at locations in Essex County, Ontario (see Figure 1).

Recorder	Location	No. of recording hours		Total number of calls*		Detections/1000 h recordings	
		Spring	Fall	Spring	Fall	Spring	Fall
Mainland 1	Holiday Beach Conservation Area	328.08	576.40	600	1840	1828.8	3192.2
Mainland 2	Private woodlot near McGregor, Ontario	328.08	521.34	1720	5282	5242.6	10131.6
Mainland 3	Cedar Creek Conservation Area	313.86	576.40	3633	5966	11575.2	10350.5
Mainland 4	Point Pelee National Park	328.08	567.15	1119	2568	3410.8	4527.9
Island 1	Fish Point Provincial Nature Reserve, southern Pelee Island	306.91	566.37	5296	6927	17255.9	12230.5
Island 2	Fish Point Provincial Nature Reserve, southern Pelee Island	328.08	576.40	653	11428	1990.4	19826.5
Island 3	Lighthouse Point Provincial Nature Reserve, northern Pelee Island	328.08	576.40	9533	3556	29056.9	6169.3
Total		2261.17	3960.46	22554	37567		

the island (Table 1). We found no evidence in the acoustic recordings that any species avoided crossing Lake Erie. In spring migration, all species or species groups were detected in both mainland and island recordings; in fall migration, American Robin (*Turdus migratorius*) and Wood Thrush (*Hylocichla mustelina*) were recorded only on the island, and a single Virginia Rail (*Rallus limicola*) was recorded on the mainland, with none on the island.

The banding data show a similar pattern in that most species or species groups were captured in both mainland and island mist nets (Table 1). In spring migration, the "double-down" species group and the Fox Sparrow (*Passerella iliaca*) / Song Sparrow (*Melospiza melodia*) species group were captured in mainland but not island mist nets, whereas Hooded Warbler (*Wilsonia citrina*), Mourning Warbler (*Oporornis philadelphia*), and White-crowned Sparrow (*Zonotrichia leucophrys*) were captured in island but not mainland mist nets.

In fall migration, the "double down" species group and the Fox Sparrow / Song Sparrow group was captured on the mainland, but not in island mist nets, whereas a Rose-breasted Grosbeak (*Pheucticus ludovicianus*) was captured on the island but not in the mainland mist nets. Several species (American Robin, Wood Thrush, and the Cuckoos) were netted in spring but not in the fall.

Date of arrival

In the spring, species were first detected significantly earlier at the island recorders than on the mainland (average ordinal date of first detection on island: 114.1 ± 1.6; mainland: 117.1 ± 1.6; Wilcoxon sign-rank test: W = 154.5, P = 0.0006, n = 36). This matched our prediction that birds would be detected earlier at the more southerly site during northward migration. However, in the fall, there was no significant difference between dates of arrival on the mainland and the island (average ordinal date of first detection on island: 254.6 ± 1.8; mainland: 258.1 ± 2.8; Wilcoxon sign-rank test: W = 73.5, P = 0.09, n = 36).

Based on data from the banding stations, we found no significant difference in date of arrival during spring (average ordinal date of first detection on island: 119.8 ± 1.8; mainland: 121.2 ± 1.9; Wilcoxon sign-rank test: W = 0.5, P = 0.99, n = 22) or fall migration (average ordinal date of first detection on island: 248.4 ± 2.0; mainland: 252.0 ± 5.0; Wilcoxon sign-rank test: W = 36.0, P = 0.28, n = 25).

Discussion

Acoustic recordings of nocturnal migrants over western Lake Erie showed that migratory birds do not avoid crossing the lake and suggest that birds may concentrate over Pelee Island mid-way across the lake on both their northward and southward journeys. Island microphones detected significantly more calls in both spring and fall than the microphones located nearby on the

north shore of Lake Erie. Migrant communities on the mainland and island were similar in composition, although subtle seasonal differences in the relative abundance of each species were evident. Species were detected by acoustic recorders earlier in the spring on the island than on the mainland. Based on the differences in the number of birds and the timing of migration, we conclude that Lake Erie does not represent an ecological barrier to migratory birds. Although our results suggest that a migratory route across Pelee Island is especially important in this region, acoustic recordings collected over the open water of Lake Erie will be required to confirm whether birds concentrate over the island during migration.

Thousands of night-flight call detections revealed a substantially greater number of calls over Pelee Island than over mainland Ontario during both spring and fall migration. This implies that birds use the island archipelago in large numbers during migration. Pelee Island's geography could act to concentrate birds as they approach the north or south tip of the island (Farnsworth 2005). Point Pelee National Park, a peninsula that projects into Lake Erie, may also concentrate birds as they migrate south in the fall (Lincoln *et al.* 1998*), although our acoustic recorder in the centre of this peninsula (Figure 1) did not detect significantly more migrants than the other mainland sites (Table 2). The theory that peninsulas concentrate migratory birds is supported by the fact that more calls were detected by the microphone at the north end than those at the south end of Pelee Island in spring and the reverse in the fall (Table 2), although this is an anecdotal observation.

We interpret the higher number of acoustic detections over Pelee Island than over the mainland in both seasons as evidence that more migrants pass over the island, but this pattern could also arise if birds increase their calling rate as they pass over islands. Although the function of night-flight calls is still under debate, they may be important in maintaining flock cohesion and communicating directional information to flockmates (Hamilton 1962; Farnsworth 2005). As birds approach a shoreline and detect open water, this may be an especially opportune time to communicate, perhaps to aid orientation among flockmates, leading to higher numbers of flight calls (Farnsworth 2005). However, confirming this pattern requires further investigation at multiple positions, such as microphones mounted in the middle of the lake away from islands, for direct comparison with island recordings. This is a challenging area for future research.

It is also noteworthy that radar research suggests that migrating birds may decrease their altitude as much as 9% when crossing bodies of water (Bruderer and Liechti 1998); this might make them more likely to be detected by our island microphones than mainland microphones and explain the greater number of calls detected on the island. However, radar data suggest that Great Lake islands are important parts of the migratory flyway (Diehl *et al.* 2003); thus, these alternative explanations alone cannot account for the higher number of migrants detected on the island.

All songbird species or species groups were detected by the island recorders in both spring and fall, and mist net data contain only subtle differences. This suggests that the lake is not an insurmountable barrier to any of the nocturnal migratory species or species groups that we studied. Previous radar studies demonstrate that nocturnal migrants cross Lake Erie in significant numbers in both spring and fall (Diehl *et al.* 2003), although they do not reveal which species are crossing the lake. All species and species groups that we could distinguish do indeed cross over Lake Erie in both fall and spring migration. Further research on seasonal variation in migration paths (especially through the use of geolocators; e.g., Stutchbury *et al.* 2009), as well as multi-year studies that explore annual variation, will provide important insight into the migration of birds through the Great Lakes.

In the spring, the first birds of each species or species group were detected earlier by the Pelee Island recorders than those on the mainland. This matched our expectation and is consistent with the seasonal direction of migration. However, contrary to our expectation, we did not find the reverse pattern during fall migration, when the dates of first detection were not statistically different at the mainland and island sites. Further investigation is required to explore whether this anomaly is due to Lake Erie serving as a temporary barrier to spring migrants, but not to fall migrants. Further examination of the stopover behaviour of birds on Pelee Island might determine whether they are spending a longer time on the island in the spring than in the fall, which might produce the significant delay in detection on the mainland. This idea stands at odds with the general consensus that the spring migration window is shorter, with many species flying faster and stopping for briefer periods (e.g., American Redstart, *Setophaga ruticilla*; Morris and Glasgow 2001). Furthermore, our banding data showed no significant differences between mainland and island sites in first arrival date in spring and fall.

Although Lake Erie may not be an insurmountable barrier to migrants, poor weather conditions may amplify the risk of crossing open water. Wind strength and direction, visibility, cloud cover, and temperature play a role in determining the intensity of migration events (Elphick 2007; Gagnon *et al.* 2011). Low cloud cover may concentrate migrants at lower altitudes, resulting in higher acoustic detection rates (Evans and Mellinger 1999). Furthermore, artificial light may cause disorientation and serve to reorient birds in flight toward the island or cause individuals to increase their calling rate (Evans *et al.* 2007; Poot *et al.* 2008). Artificial light may have a more pronounced effect under poor or deteriorating weather conditions when stars are obscured by cloud cover (Farnsworth and Russell 2005; Hüppop

and Hilgerloh 2012). An investigation into the composition of nocturnal migrants detected over Pelee Island on nights preceding and during strong winds or precipitation could lead to a better understanding of which species are most affected by poor weather while navigating the Great Lakes.

In the western basin of Lake Erie, acoustic and banding data suggest that Pelee Island is an important geographic feature for migratory birds. Many individuals of all species passed over the island in spring and fall, with little indication that they avoided crossing Lake Erie, suggesting that islands in the middle of potential geographic barriers are important for migratory birds. Given that many species of North American migrants are in decline, studies that monitor migratory bird behaviour at smaller geographic scales are important for local management and development decisions in regions where birds are known to concentrate seasonally.

Acknowledgements

We thank M. Watson for assistance in collecting recordings. We thank C. Berek, A. Demarse, K. Drca, R. Gough, C. Lajoie, J. Mahal, A. Mamo, L. Mehdi, B. Poisson, M. Watson, and A. Weinz for assistance with annotating recordings. We thank the Holiday Beach Migration Observatory for their ongoing volunteer-based efforts to study avian migration in southwestern Ontario. We appreciate the work of bird banders on Pelee Island, and we thank the Canadian Wildlife Service of Environment Canada for providing banding data from Pelee Island. We thank the Essex Region Conservation Authority, Ontario Parks, and Parks Canada for access to conservation areas and parks. We thank C. Francis and an anonymous reviewer for comments that improved this manuscript. Support for this study was provided by the Natural Sciences and Engineering Research Council of Canada, the Canada Foundation for Innovation, the Government of Ontario, the University of Windsor, and Caldwell First Nation.

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Received 7 October 2013
Accepted 20 November 2013

Parental Care by Lone Male Ferruginous Hawks (*Buteo regalis*), Rough-legged Hawks (*Buteo lagopus*), and Great Horned Owls (*Bubo virginianus*) was Limited to Providing Food

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Schmutz, Josef K., Martin A. Gérard, Gordon S. Court, and R. Wayne Nelson. 2014. Parental care by lone male Ferruginous Hawks (*Buteo regalis*), Rough-legged Hawks (*Buteo lagopus*), and Great Horned Owls (*Bubo virginianus*) was limited to providing food. Canadian Field-Naturalist 128(2): 145–150.

In three long-term studies of Ferruginous Hawks (*Buteo regalis*), Rough-legged Hawks (*Buteo lagopus*), and Great Horned Owls (*Bubo virginianus*), we observed rare but regular occurrences of superabundant prey at nests where nestlings were hungry, emaciated, or dead. In these cases, a male appeared to be the lone parent; the female parent was found dead, kept away by disturbances, or simply absent. We conclude that the male parents, whose normal role is to provide food, were unable to expand their care to include morseling, feeding, and brooding. Faced with the stress of incessant food begging by nestlings, the male parents responded by bringing more and more food to the nest, to the point where food spoiled while the young starved amid plenty. We provide and interpret detailed observations for 11 such cases and suggest several variables that would influence the nestlings' chances of survival.

Key Words: Ferruginous Hawk; *Buteo regalis*; Rough-legged Hawk; *Buteo lagopus*; Great Horned Owl; *Bubo virginianus*; parental care; food provisioning; feeding; brooding; starvation; Rankin Inlet; Nunavut; Hanna; Alberta; Saskatoon; Saskatchewan

Introduction

Studies of birds have revealed fascinating patterns of mate choice and parental care, including elucidation of the apparent ecological correlates that predictably lead to such patterns (e.g., Cockburn 2006). Typical patterns include brood parasitism; male only, female only, and bi-parental care; and cooperative breeding (Cockburn 2006).

Care of young by monogamous pairs is the most common pattern among raptors and birds in general; 81% of all species exhibit it. Among raptors, three overlapping phases occur: at first, the female assumes brooding and shading duties almost continuously; later, the female leaves the partly grown young for part of the time to roost or even hunt nearby; and, finally, both male and female may be away hunting when the young approach fledging (Newton 1979, page 160).

A difference in body size influences the way in which dominance relationships and parental roles are apportioned within a raptor pair. Although a difference in size between females and usually larger males is common among animals (e.g., Blanckenhorn 2005), this is reversed among raptors with females about a third larger than males (e.g., Olsen and Olsen 1987). The nest is the female's domain, and it is common among broad-winged hawks, and possibly less so among falcons, for the male to spend little time at the nest (Newton 1979, page 159).

Using an inductive style of inquiry (e.g., Schmutz 1992), we report on observations at nests and emphasize context and detail in our field observations and related literature. We examine a male's limits in parental care and ask whether a male parent can adequately compensate for the loss of a female and under what conditions this may be possible.

Study Area and Methods

Ferruginous Hawks (*Buteo regalis*), studied near Hanna, Alberta, were in moist, mixed-grass prairie where rangeland grazing of cattle was the dominant land use. Richardson's Ground Squirrel (*Urocitellus richardsonii*) was the hawks' main prey. Our observations were part of a long-term population study varying in intensity from banding and monitoring of breeding densities each year to detailed monitoring of prey, growth of nestlings, and survival and dispersal of colour-marked young and breeding adults (Schmutz *et al.* 2008). The number of nests and visits to nests varied accordingly, from near daily during the nestling period to once a season. The use of an intensively studied core area and a peripheral area also affected the number of visits.

Observations of Rough-legged Hawks (*Buteo lagopus*) were made in the vicinity of Rankin Inlet, Nunavut, within an area defined for the long-term investigation of the breeding biology of Arctic Peregrine Falcons (*Falco peregrinus*; Court *et al.* 1988).

Great Horned Owl (*Bubo virginianus*) studies were conducted from a base in Saskatoon, Saskatchewan. Nests were reported by area residents or spotted from roads while trees were still devoid of foliage. Once located, nesting areas were visited annually to determine occupancy. Owlets were banded and prey items recorded (Gérard *et al.* 2009).

For convenience, we refer to cases or nests by number, preceded by F, R, or G, for Ferruginous Hawks, Rough-legged Hawks, and Great Horned Owls, respectively (Table 1).

Results

Observations of parental care deficits were rare in our studies (< 1% in over 5000 visits to all nests) and occurred at different stages in the nestling period and in different years.

Ferruginous Hawk nests

F-1: On our arrival at the study site on 9 June 1975, two nestlings less than 1 week old were peeping as if hungry, although prey was in the nest and a dark morph female, judging by size, was roosting on the nest rim. On 11 July, both nestlings were dead, a light morph Ferruginous Hawk was circling overhead, and the dark morph bird was not seen. In the nest, we found 14 dead Richardson's Ground Squirrels. Our interpretation was that the nestlings vocalized out of hunger, to which the male parent responded by bringing more food but did not feed them.

F-2: On 30 June 1989, a mass of about 20 Richardson's Ground Squirrels was found in a nest used during that year, but without young or adults visible at the time. Many of the squirrel bodies were whole. They had decayed and dried, suggesting that they had been captured and deposited 2–3 weeks earlier. This would have placed the prey deliveries about mid-way through the normal nestling period for Ferruginous Hawks in that year.

F-3: On 11 June 2002, a nest with two nestlings and no prey was attended by a light morph Ferruginous Hawk circling overhead. On 4 July, one nestling was dead and one alive. The live nestling gave monosyllabic, flutelike calls suggesting hunger (see Powers 2003, page 98). Of 30 partial or whole ground squirrels in the nest, 11 were gutted but otherwise uneaten, yet no parent was visible. The live nestling weighed 905 g at a primary length of 150 mm, the dead nestling 600 g at 132 mm (see Schmutz 1977, Appendix 3 for age determination). Assuming that the emaciated nestlings were smaller-bodied males, they were still 180 and 470 g below normal weight for their age, respectively. The most plausible interpretation was that one nestling had starved to death and the second was near death.

F-4: On 8 June 1976, a single, distant adult called in defence of a nest where a 410-g nestling emitted peeping sound (presumed hunger), although seven Richardson's Ground Squirrels were present. On 10 June, the nestling was dead with the prey still in the nest. We

TABLE 1. Summary of nestling care deficits and reproductive outcomes for four Ferruginous Hawk (*Buteo regalis*) nests near Hanna, Alberta, two Rough-legged Hawk (*Buteo lagopus*) nests near Rankin Inlet, Nunavut, and five Great-horned Owl (*Bubo virginianus*) nests near Saskatoon, Saskatchewan.

Nest no.	Parents	Nestling age	Nestling status	Prey in nest	Nestling outcome
Ferruginous Hawk nests					
F-1	Male, possibly both	1 week	Hungry then died	In excess	Died
F-2	None, nest abandoned	Unknown	Unknown	In excess	Presumed dead
F-3	Male only	28 and 30 days	Starving	In excess	1 died, 1 fostered
F-4	Lone parent	11 days	Hungry, dead 2 days later	In excess	Died
Rough-legged Hawk nests					
R-1	Parents known present	3 weeks	Unfed for lengthy photography periods	In excess	Lived
R-2	Male only female presumed dead	3 weeks	Starving	In excess	2 of 3 dead
Great-horned Owl nests					
G-1	Male only Female electrocuted	2–3 weeks	Hungry	1 meadowlark	Survived ≥ 7 days
G-2	Male only	3 weeks	1 dead, 1 snow covered and hungry	1 magpie	Unknown
G-3	Male only Female dead 10 days	4 weeks	No apparent care	2 birds 1 rabbit	Survived 3 weeks to fledging
G-4	Male only	4 weeks	1 dead 3 hungry	In excess	Unknown
G-5	Male only	4 weeks	No apparent care	In excess	Apparently healthy 6 days later

assumed that a nestling reared to 11 days must have had a female parent initially, and, later, the remaining adult was a male unable to feed the nestling.

Rough-legged Hawk nests

R-1: From 29 to 31 July 2000, a blind was installed for photographic purposes approximately 15 m from the nest of a pair of Rough-legged Hawks, about 10 km north of Rankin Inlet, Nunavut. The pair had three young, approximately 3 weeks of age. Each member of the pair was easily identified to sex based on plumage. The adult male was apparently not affected by the installation of the blind and delivered several Siberian Brown Lemmings (*Lemmus sibiricus*) to the nest each day when photographers were present. At no time was the male observed attempting to feed nestlings, and the nestlings did not feed themselves. The adult female did not attend the nest when photographers were in the blind, and no feedings were witnessed during photographic sessions lasting up to 6 h. The young were apparently fed by the female after the photographers' departure; when the photographers arrived to film each day, the previous day's food was absent and the female flushed on their arrival. We recorded several prey deliveries by the adult male over the 3 days. Our interpretation at the time was that male Rough-legged Hawks do not feed young despite ample opportunity and apparent need.

R-2: On 8 August 2005, a visit to a Rough-legged Hawk nest on the Barrier Islands, Rankin Inlet, revealed only an adult male present. The female parent was not recorded at the territory during the visit, which lasted more than 1.5 h, unusual for this species at this location and time of year. The nest contained one live but emaciated nestling and two dead nestlings that were extremely emaciated and had apparently starved to death (Alastair Franke, Research Associate of the Circumpolar Institute at the University of Alberta and the Principal Investigator for Arctic Raptors, personal communication, 8 August 2005). The living nestling was standing on or beside the carcasses of at least five uneaten Arctic Ground Squirrels (*Spermophilus parryii*) and one Siberian Brown Lemming. We concluded from these observations that the female had died and that the male was not feeding the starving young, despite the availability of ample prey.

Great Horned Owl nests

G-1: On 29 April 2002, a telephone call alerted us to three orphaned Great Horned Owl nestlings. On 26 April 2002, a female had been electrocuted on a transformer, which subsequently required repair. On MAG's arrival, a male flushed from a roost and came to within 5 m of the nest tree in a farm shelterbelt. Three young, approximately 12, 16, and 20 days old, were in the nest, along with a whole, fresh, male Western Meadowlark (*Sturnella neglecta*). As the young were making hunger calls, MAG fed the meadowlark to the two larger owlets. The youngest owlet was removed and introduced into a foster nest with only one nestling near Saskatoon. On 1 and 3 May 2002, the remaining two young were reportedly doing well. We assume that the two nestlings were large enough to feed themselves, possibly by consuming small prey whole.

G-2: On 6 May 2002, a nest 6 m above ground in a Trembling Aspen tree (*Populus tremuloides*) was snow covered after a snowstorm the previous day. The nest contained a freshly dead, 400-g Great Horned Owl nestling and a shivering 660-g nestling, plus the whole, fresh carcass of a Black-billed Magpie (*Pica hudsonia*). The living chick appeared to be cold and was "chittering" continuously. It readily ate offered morsels of the magpie. A shy adult male owl was observed nearby — apparently the sole survivor of the nesting pair — and was behaviourally unable to brood and tear prey for the nestling. We believe we saved or prolonged the life of the second nestling by removing snow and feeding it.

G-3: On 13 May 2005, a female owl that had been banded at this nesting area in 2002 was found dead below a nest containing one young. The female was partly decomposed and estimated to have been dead for 7–10 days. Prey, including a blackbird (Icterinae), a rabbit head (Lagomorpha), and a Grey Partridge (*Perdix perdix*), were on the ground below the nest, and a shy Great Horned Owl, judged by size to be a male, was nearby. At banding time on 2 June 2005, the estimated 7-week-old fledgling owl flew poorly. The adult male was still present and being mobbed by American Crows (*Corvus brachyrhynchos*). It was protective of the young and aggressive toward our black Labrador dog. By removing the dead female, we may have encouraged the male to place prey in the nest subsequently.

G-4: On 6 May 2008, we observed a nest containing one dead and three live owlets, estimated to be 25, 28, and 30 days old. An adult owl attended the nest, but without venturing from nearby cover. The young were vocalizing as though hungry. The nest contained three young Snowshoe Hares (*Lepus americanus*), five Northern Pocket Gophers (*Thomomys talpoides*), one Northern Shoveler (*Anas clypeata*), one Long-eared Owl (*Asio otus*), and the remains of a Northern Harrier (*Circus cyaneus*). The hungry young consumed a whole hare and part of the shoveler when these were offered in morsels. The smallest nestling was fed and introduced into a foster nest attended by two adults. We took signs of hunger despite superabundant food to indicate that parental care was compromised. All remaining prey appeared to be too large for the young to swallow whole or tear apart on their own.

G-5: On 5 May 2012, two 4-week-old owls were banded. Their nest contained eight American Coots (*Fulica americana*), one Gadwall (*Anas strepera*), one rabbit, and one Virginia Rail (*Rallus limicola*). Some of the coots contained maggots. A male adult owl was in attendance. Several days later, the nest was revisited and, again, only a male was in attendance. At 4 weeks

of age, we assumed that the young owls were able to feed themselves, possibly swallowing small prey when offered while leaving the large coots, ducks, and rabbit uneaten.

Discussion

Is the male's parental care role inflexible?

A common theme throughout these observations was food in all 11 nests and so much excess food that it spoiled in five of them (Table 1). Another common feature was the presence of a male parent only, except in nests R-1 and, possibly, in nest F-1 with F-2 unknown. Adult gender was judged based on raptor size, plumage, in-hand inspection (G-1, G-3), in-flight/roosting observation (F-1, G-2), or presumed based on the fact that the food-provision role (male) was satisfied while the brooding and feeding role (female; Bechard and Schmutz 1995; Houston *et al.* 1998; Bechard and Swem 2002) was not (F-3, F-4, R-2, G-4, G-5).

We know that two females had died (G-1, G-3). We assume that other females had also died (F-1, F-2, R-2, G-2, G-4, G-5) or that they were somehow kept away from the nest (e.g., R-1). Nestlings were starving, hungry, or cold, indicating that females were absent for at least several crucial hours (e.g., during a snowstorm) and for the days it took the males to amass excess prey, some of which had begun to spoil. We concluded that the female member of the pair was lost and that the male was induced to keep hunting by the hungry young. Males were unable to make the needed shift to feeding and brooding.

We are cognizant of the additional possibility that some nestlings may have died because of congenital problems or poisons in the environment (e.g., Schmutz *et al.* 1989) and that such nestlings voice physical pain, which would induce the male to continue hunting. This is unlikely in cases where nestlings survived or were transplanted (F-3, G-1, G-3, G-5). In case of F-3, the surviving nestling fledged from its foster nest, although, later, its long-dead carcass was found. Its early near starvation state may have compromised normal development, preventing this nestling from maturing normally and becoming able to hunt and survive on its own.

Flexible parental roles in related species

Kenward (2006) summarizes observations and reports that suggest some Northern Goshawk (*Accipiter gentilis*) males are also unable to care fully for their young when the female is lost. As in our cases, young starve in the face of ample food. Also similar to some of our owl cases, however, young Goshawks fledged from five nests where females disappeared at nestling age 12–20 days, when they begin to feed themselves.

When nestlings are very young and exposed to weather, the ability of their parents to brood is as important to their survival as the availability of food. In nest G-2, we believe that the failure of the male owl to brood the young during a snowstorm led to the death of one nestling; the other was likely saved by our clearing snow off the nest. For comparison, RWN has observed a male Peregrine Falcon flying to a nest when the female had left temporarily and begin to cover and brood the young. Similarly, JKS observed a male Swainson's Hawk (*Buteo swainsoni*) cover the eggs in a nest after the male had brought prey which the previously incubating female accepted from him and ate atop a fence post.

In clear contrast to our observations of limited parental care, a study of a captive male Red-tailed Hawk (*Buteo jamaicensis*; Hamerstrom and Hamerstrom 1971) suggests that males of this species can participate in all facets of reproduction. The hawk studied had been taken from its nest at the nestling stage and used for falconry. Its gender was confirmed by ejaculation elicited by the falconer on whom the hawk was imprinted. The male hawk wove sticks into a nest base, formed a lined nest cup when straw was provided, covered a chicken egg, and developed a 5-cm × 6-cm brood patch, but without significant blood vascularization. The male hawk accepted a total of three Red-tailed Hawk nestlings 1, 6 and 21 days old offered over 2 years. Without prior experience, it responded positively to the vocalizations of the newly introduced 1 and 6-day-old nestlings and displayed great care closing its talons and sliding mostly on his tarsus over the nestlings to brood. It fed the nestlings pieces of flesh until they were 9 days of age. The pieces were not regurgitated, but still moist from saliva that seemed to flow more during feeding. After 9 days, the male tended to lay small pieces of meat on the nest rim for the nestlings to eat. By 24 days, the nestlings began to tear and consume mice and day-old chickens on their own. When the nestlings were 16 days old, the male gradually stopped brooding them at night, in a mid-May Wisconsin climate.

It may be surprising that hawks of the same genus differ so greatly in terms of parental care. The Red-tailed Hawk described above capably conducted all facets of parental care, including the development of a rudimentary brood patch. In contrast, we observed Ferruginous and Rough-legged Hawks, and Great Horned Owls, fail to tear prey and feed morsels to begging nestlings, a simple act that might have prevented their starvation. Species-specific behaviour repertoires may vary to that extent. Another possibility is that plasticity in parental care exists initially, but is lost through experience and discouraged by the dominant female.

Are female roles similarly inflexible?

At a different nest, a series of observations suggested that a female Ferruginous Hawk was able to assume the food provisioning role of males and raise her brood alone. Here, a male was observed with the female on two visits (6%) just before eggs hatched, then not again for the remaining 32 visits during the nestling period. This deviated from the typical pattern of two adults defending a nest in 38% of 164 visits in 1975 ($G = 9.42$, $P = 0.002$). Prey was less often present in the female-only nest, on only 21% of 29 nest checks

compared with 54% of 420 visits ($G = 10.77$, $P = 0.001$) to all other nests. Despite the lone attendance of the female parent and scarce prey in the nest, the young appeared as well fed as others. At least one young had food in its crop on 57% of 7 crop records, compared with 41% of 96 crop records ($G = 0.72$, $P = 0.396$) from nests with both parents in attendance.

These results suggest that this female Ferruginous Hawk was able to both hunt and care for her young, raising two young from four eggs to fledging. She likely left her young exposed during favourable weather, hunted when the young were hungry, and fed them immediately on return. This pattern would account for the reduced frequency at which food was found in the nest, yet also account for well-fed young with an average rate of food present in their crops. This male-loss or abandonment occurred in a year of exceptional food availability (Schmutz *et al.* 2008).

Is the mating system of Ferruginous Hawks female-centred?

In a female-centred mating system, the male is not only dependent on the female for reproduction, but also takes its cues from the female. Some observations suggest that this is the case in Ferruginous Hawks.

Observations from a blind in 1990, by Janet Foster (co-owner of John and Janet Foster Productions Ltd., personal communication, 26 June 1990) confirm the nestling-care role of females (see also Powers 2003). On several occasions, all four nestlings patiently waited their turn without struggle to be fed. Only once did two or more nestlings pull on the same piece of food offered by the female. When the offered piece of food was too large and the nestling struggled to swallow, the female took it back and ate the food herself. These nestlings were 28–31 days old at the time.

Older nestlings are able to feed on their own. Observing the same nest as above from a blind in 1989, Dan Wood (owned Wild Prairie Photographics Ltd., personal communication, 7 July 1989) observed a male, judging by size, leave a hill where it and the female had been roosting. The male returned 1 h later and delivered a ground squirrel directly to the nest, and then rejoined the female on the hill. One of the three young took the delivered ground squirrel from the nest rim and eventually all three nestlings fed on their own at ages 39 and 41 days.

A film sequence taken without audio in 1990 at the nest mentioned above shows male and female Ferruginous Hawks roosting side by side on the nest rim (Foster and Foster 1992*). Twice, the female turned her head toward the male with crown feathers erect and beak opening, suggestive of a dominance cue, whereupon the male left the nest to land on a branch in the same tree only 2 m away. This behaviour combined with the pattern of a male's rare and brief presence at nests with young, suggests that the female discourages the male from tending young.

Other observations support the female's primary role where the nest and young are concerned. In dozens of images obtained using time-lapse photography of nests (JKS, unpublished), in only one case did both male and female roost on the nest rim together; usually it is only the female. Similarly, Powers (2003) describes adult males delivering prey directly to the nest, as described by Dan Wood above, but "he never tarried at the nest but sat only briefly before departing within a few seconds of his food delivery, presumably to hunt for more food" (Powers 2003, page 67). Powers (2003, page 93) concluded that a male remained only 5–15 s at a nest after a prey delivery, and the longest observed stay was 5 minutes.

In the context of the female's primary care at the nest and, possibly, even enforced dominance over the male, the F-3 male's inability to channel its care away from excessive hunting to feeding is plausible. Repeated exclusion from the nest by a female, possibly over several years, likely reinforced nest avoidance, and flexibility in nestling care, if any, was lost through learning. This role development with experience and learned irreversibility could also apply to Great Horned Owls and Rough-legged Hawks.

Female loss and prey size

Our observations suggest that three broods of Great Horned Owls (G-1, G-3, G-5) survived in the absence of a female. Large owls and especially Great Horned Owls are known for their ability to swallow sizeable prey whole. This could have been a significant factor in the survival of some of the owl broods after female loss. Furthermore, the prey used by the owls was varied and included smaller items such as voles, mice, and songbirds.

In contrast, the diet of Ferruginous Hawks and Rough-legged Hawks (R-2) included primarily relatively large, tough-skinned ground squirrels. Our observations of the Ferruginous Hawks showed that 28–31-day-old nestlings still waited for the female to feed them. At 39–41 days, nestlings tore ground squirrels and fed on their own.

Nests F-3, F-4, R-2, G-2, and G-4 are noteworthy as nestlings were hungry and even starving amid plenty of food. The F-3 nestlings were an estimated 28 and 33 days old, and apparently could not tear and consume the ground squirrels that were present. The older starving nestling may have tried to eat on its own as it had dried blood on its beak.

Even with females present, a parental miscue was noted by Wayne and Alora Nelson (personal communication). A captive, 9-year-old, human-imprinted female Ferruginous Hawk incubated and tended to her hatchling normally, but persisted in presenting food morsels 5 cm above the nestling's beak. The Nelsons had to feed the young until it was 1 week old and able to touch the female's beak, which led to normal feeding by the female soon after.

In conclusion, we suggest that starving nestlings amid a superabundance of food in nests is a rare but widespread occurrence and that, in these cases, the loss of the female parent should be considered. We also provide evidence that male loss is less severe than female loss. Furthermore, we suggest several variables that might influence reproductive outcome after female loss: age of nestlings, prey size related to the ability of nestlings to swallow it whole, and, possibly, age of the male parent. We postulate that first-breeding males may exhibit more behavioural flexibility in feeding young than males whose role as a mere provider has been entrenched by the female over several breeding seasons.

Acknowledgements

We thank landowners for access to their land and helpful information. We were assisted in the hawk study by John and Janet Foster, Arnold Grandt, David Moody, Skylar Rickabaugh, and Dan and Gwen Wood and in the owl study by Jean and Keith Harris, Stuart and Mary Houston, Sig Jordheim, Art Lepp, Bruce and Hilda Noton, Glen Peterson, Kevin and Bergit Pulvermacher, Dennis Siegel, Marten Stoffel, Glen and Mary Walker, and Dan Zazelenchuck. Alastair Franke (arcticraptors.ca) provided access to the hawk nest at Rankin Inlet in 2005; the Department of Sustainable Development, Government of Nunavut, provided access to the nest visited in 2000. Ricardo A. Figueroa, André Gérard, Matthew D. Giovanni, Lynn W. Oliphant, Katherine McKeever, and three anonymous reviewers provided helpful comments on the manuscript.

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Received 25 October 2013
Accepted 11 January 2014

Apparent Widespread Decline of the Boreal Chorus Frog (*Pseudacris maculata*) in Eastern Ottawa

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Seburn, David C., Kari Gunson, and Frederick W. Schueler. 2014. Apparent widespread decline of the Boreal Chorus Frog (*Pseudacris maculata*) in eastern Ottawa. Canadian Field-Naturalist 128(2): 151–157.

The Boreal Chorus Frog (*Pseudacris maculata*) was once common in the eastern Ottawa area. To assess its current status, we conducted auditory surveys at 184 wetlands in 2011 and 2012. Boreal Chorus Frogs were heard at only five (2.7%) of the surveyed sites. These five sites were spatially aggregated, with only 0.5–7.5 km between any two sites. Sites occupied by Boreal Chorus Frogs in eastern Ottawa were surrounded by significantly greater agricultural cover (at 1.0-, 1.5-, and 2.0-km radii), less forest cover (1.0- and 2.0-km radii), and less wetland cover (1.5- and 2.0-km radii) than occupied sites in western Ottawa. Sites in eastern Ottawa that were apparently unoccupied were surrounded by significantly greater agricultural cover (only at the 2.0-km radius), similar forest cover (all radii), and less wetland cover (all radii) compared with occupied sites in western Ottawa. Boreal Chorus Frog populations are commonly subject to extirpation resulting from stochastic events. The reduced wetland cover in eastern Ottawa may be accompanied by reduced wetland connectivity, making recolonization of wetlands difficult or impossible. Our data do not show whether wetland connectivity has been reduced, but future research should address this important topic.

Key Words: Boreal Chorus Frog; *Pseudacris maculata*; amphibian decline; Ottawa; Ontario; amphibian habitat; wetland connectivity

Introduction

Amphibian populations are known to be declining around the world (Wake and Vrendenburg 2008; Collins and Crump 2009; Collins 2010). A global assessment of all known amphibian species revealed that a third were threatened with extinction (Stuart *et al.* 2004). Although multiple causes have been identified, land use change resulting in habitat destruction is the leading cause of amphibian decline and extinction (Collins and Crump 2009; Collins 2010). Amphibian populations have also declined within protected areas where habitat destruction is not a threat. Such declines have been linked to numerous factors including introduced fish species (e.g., Knapp and Matthews 2000), disease (e.g., Rachowicz *et al.* 2006), pesticide drift (e.g., Davidson 2004), and climate change leading to reduced hydroperiod in temporary wetlands (e.g., McMenamin *et al.* 2008). In addition, sublethal effects of contaminants such as pesticides may make amphibians more susceptible to diseases (e.g., Davidson *et al.* 2007).

In eastern Ontario and western Quebec the Boreal Chorus Frog (*Pseudacris maculata*), formerly assigned to the species Western Chorus Frog (*P. triseriata*), has undergone substantial declines. It was once considered common southeast of Montréal (Bleakney 1959), but now appears completely absent from that area (Daigle 1997) and is extremely rare in Quebec (Desroches and Rodrigue 2004; COSEWIC 2008*). It has also become less widespread in areas of northern New York state (Gibbs *et al.* 2005; Corser *et al.* 2012) and eastern Ontario near Cornwall (Seburn *et al.* 2008) and appears to have been extirpated from Vermont (Andrews 2013). Largely as a result of declines in Quebec, the Great Lakes/St. Lawrence–Canadian Shield population (under the name Western Chorus Frog) was designated threatened by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC 2008*).

The trilling chorus frogs form a clade of closely related species within the genus *Pseudacris* (Moriarty and Cannatella 2004). A range-wide analysis of the mitochondrial DNA of trilling chorus frogs substantially revised our understanding of species limits in this group and determined that populations in eastern Ontario and western Quebec should be assigned to the Boreal Chorus Frog species (Lemmon *et al.* 2007). These taxonomic changes have been widely accepted (e.g., Corser *et al.* 2012; Dodd 2013), which requires that the literature on trilling chorus frogs be examined carefully to determine the current species allocation. Even recent papers (e.g., Sacerdote and King, *in press*) do not always follow the current taxonomy.

Recent surveys of the Boreal Chorus Frog in eastern Ontario have produced mixed results. Boreal Chorus Frogs were detected at only 5% of historical locations surveyed in the Cornwall area (Seburn *et al.* 2008), yet were found at two-thirds of historical locations in western Ottawa (Seburn and Gunson 2011), approximately 100 km away. The cause (or causes) of the declines remains unknown. Although wetland destruction is a major threat in some areas of Quebec (Daigle 1997;

Picard and Desroches 2004*), populations have also been lost in areas where wetlands remain (Gibbs *et al.* 2005, Seburn *et al.* 2008, Seburn and Gunson 2011).

The Boreal Chorus Frog is known to have been widespread east of urban Ottawa during the late 1950s and early 1960s, although precise locations are mainly lacking. Knowledge of the distribution is based largely on surveys conducted by herpetologist Sherman Bleakney (1959) and Anne and Garnet Hanes (personal communication) (Figure 1). The agonistic or territorial call of a Spring Peeper (*Pseudacris crucifer*), which is also a trill (COSEWIC 2008*), can be confused with the call of the Boreal Chorus Frog, but it is unlikely that the experienced surveyors of the 1950s confused these two species.

The first indication that Boreal Chorus Frogs were rare east of urban Ottawa resulted from a survey conducted by one of us (FWS) along with Aleta Karstad (Bishops Mills Natural History Centre) and the late Mike Rankin (Canadian Museum of Nature) from 27 to 30 April 1997. Although Spring Peepers were detected at 34 sites, Boreal Chorus Frogs were detected at only two sites (FWS, unpublished data). To assess the current distribution of the species across this area, we undertook extensive auditory surveys of roadside wetlands and flooded ditches. We hypothesized that land cover variables, particularly differences in wetland, forest, and cropland cover, might explain why the Boreal Chorus Frog was rare in eastern Ottawa and beyond compared with western Ottawa. As nitrate levels of 10 mg/L or more can cause significant mortality of Western Chorus Frog tadpoles (Hecnar 1995), we obtained surface water-quality data to determine whether nitrate contamination was contributing to local Boreal Chorus Frog decline.

Study Area and Methods

All surveys were conducted in suburban and rural eastern Ottawa and western Prescott and Russell county (Figure 2), an area of just over 800 km^2. Daytime auditory surveys were conducted during the calling season of the Boreal Chorus Frog in 2011 (11, 12, 19, 22, and 27 April) and 2012 (20, 21, 22 March and 12, 13, and 18 April). A known site with Boreal Chorus Frogs in western Ottawa was visited at the start of each survey to confirm calling was occurring that day. Although Boreal Chorus Frogs in some populations may not call consistently during the day (FWS, personal observation), diurnal surveys in western Ottawa suggest that calling is widespread even among small populations (Seburn and Gunson 2011). Auditory surveys were conducted at wetlands and flooded ditches visible from roadsides, with the exception of a few locations in public parks where wetlands away from the road could be monitored. Surveys lasted 2–5 minutes per site depending on weather conditions and traffic noise.

We obtained records of 2012 surface water (0.5 m depth) nitrate and nitrite levels from monitoring stations across Ottawa from the City of Ottawa. Because nitrate can be reduced to nitrite in biological systems (Hecnar 1995), we pooled the readings for both compounds for our analyses. As the City of Ottawa moni-

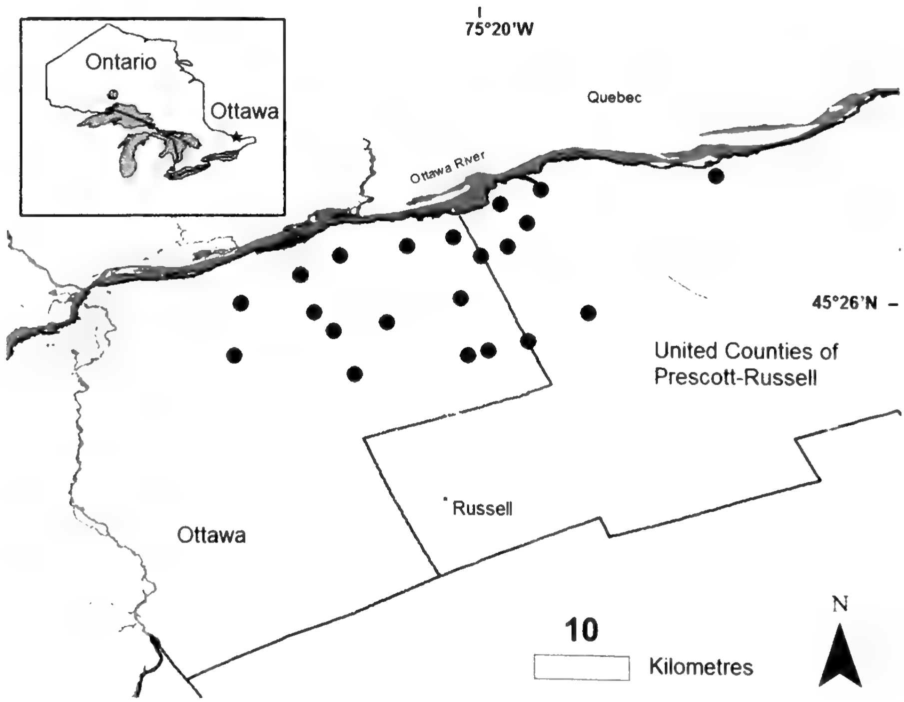

FIGURE 1. Historical records of the Boreal Chorus Frog (*Pseudacris maculata*) in eastern Ottawa and western Prescott and Russell. Localities were approximated from an unpublished map prepared by Anne and Garnet Hanes that included sites from their auditory surveys conducted in 1962 and records from Bleakney (1959) and the Canadian Museum of Nature.

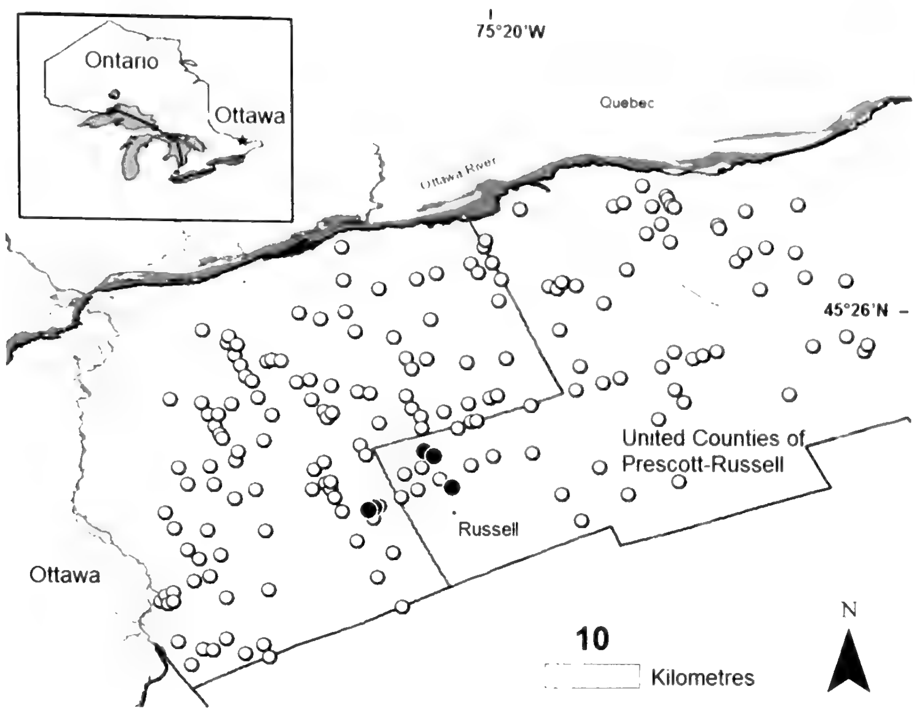

FIGURE 2. Location of 184 sites, at which auditory surveys were conducted in spring 2011 or 2012 or both, in eastern Ottawa and western Prescott and Russell. Open circles indicate sites where the Boreal Chorus Frog (*Pseudacris maculata*) was not detected; filled circles indicate the five sites where it was detected.

tors water quality a number of times during the year at each monitoring station, we took the highest combined reading of nitrate and nitrite for each station.

The Ontario Land Cover Data Base, 1st edition (Spectranalysis 1999*) was used to distinguish types of agricultural cover, specifically to separate old field/pasture (a habitat that can support Boreal Chorus Frogs) from cropland (a habitat not suitable for Boreal Chorus Frogs). This database uses spectral character obtained from satellite images to classify land cover. Land use information was also obtained from the Southern Ontario Land Resource Information System (SOLRIS). The layer represents the landscape in 15 m × 15 m pixels and is derived from a combination of satellite images, topographic maps, and aerial photographs from 2000–2003 (OMNR 2007*).

Three land use classes were used for analyses: forest cover (> 60% tree cover, including plantations), wetlands (≥ 0.5 ha in area), and agriculture (a broad category that includes intensive croplands as well as old fields and forest opening). We calculated the percentage of land devoted to each land use class for areas of radii 0.5, 1.0, 1.5 and 2.0 km around each survey site. Land use variables on a larger scale may be correlated with frog landscape ecology (e.g., Gibbs *et al.* 2005), but in this case, a larger radius would result in some areas extending across the Ottawa River into adjacent Quebec, which did not seem ecologically meaningful. Land use data from sites in eastern Ottawa were compared with known Boreal Chorus Frog sites in western Ottawa (Seburn and Gunson 2011). ArcMap 10.0 (Esri, Redlands, Cal.) was used for all spatial analyses and Minitab 8.3 (Minitab Inc., State College, Pennsylvania) for all statistical analyses.

Results

Auditory surveys were conducted at 144 locations in eastern Ottawa and western Prescott and Russell in 2011. In 2012, auditory surveys were conducted at 48 of the 144 sites (33.3%) surveyed in 2011 as well as 40 additional sites in the area. In total, 184 sites were surveyed at least once during the two years (Figure 2). No Boreal Chorus Frogs were heard at any location in eastern Ottawa and western Prescott and Russell in 2011. One of us (FWS) heard Boreal Chorus Frogs calling near Russell during other amphibian surveys on 23 March, 2012 (Karstad *et al.* 2012; Schueler and Karstad 2012*). Subsequent surveys focused on that area to attempt to locate additional sites with Boreal Chorus Frogs. In total, Boreal Chorus Frogs were heard at five of the 184 sites (2.7%) surveyed. Eight of the 48 sites (16.7%) surveyed in both 2011 and 2012 had no standing water in 2012. One additional 2011 site was in the process of being tile drained when surveyed in 2012. Only one of the 48 sites (2.1%) surveyed in both years had Boreal Chorus Frogs calling in 2012 but not 2011.

Maximum combined nitrate and nitrite level in surface water was 6.6 mg/L in eastern Ottawa and 6.2 mg/L in western Ottawa. There was no significant difference

between the combined nitrate and nitrite levels in eastern Ottawa (median = 1.6 mg/L, n = 34) and in western Ottawa (median = 1.7 mg/L, n = 25; W = 816.0, P = 0.315).

Ground truthing of cropland cover identified by the Ontario Land Cover Data Base indicated that this database was not reliable. For example, one known Boreal Chorus Frog site in an old field habitat was classified as 59% cropland. Therefore, all subsequent analyses used only the SOLRIS database.

The five eastern Ottawa sites with Boreal Chorus Frogs were clustered in three patches in an area near Russell (Figure 2). The distance between these occupied sites ranged from 0.5 km to 7.5 km, and all sites were separated by at least one road. Despite this spatial aggregation, land use varied across the five sites. For the surrounding area within a 1.0-km radius, median agricultural cover was 64.8% (range: 52.6–75.0%), median forest cover was 3.7% (range: 2.7–23.4%), and median wetland cover was 11.2% (range: 3.6–28.2%).

The occupied sites in eastern Ottawa had significantly greater agricultural cover (within a 1.0-, 1.5-, and 2.0-km radii), less forest cover (1.0- and 2.0-km radii), and less wetland cover (1.5- and 2.0-km radii) than occupied sites in western Ottawa (Table 1). Sites in eastern Ottawa that were apparently unoccupied had significantly greater agricultural cover (only for a 2.0-km radius), no significant difference in forest cover (all radii), and less wetland cover (all radii) compared with occupied sites in western Ottawa (Table 2). Many of the eastern Ottawa sites had low percentages of wetland cover. For example, although median wetland cover values for a 2.0-km radius differed by only 2.1%, 30% of eastern Ottawa sites had < 10% wetland cover, compared with only 14% of the western Ottawa sites.

Occupied sites in eastern Ottawa had greater agricultural cover (2.0-km radius only) than apparently unoccupied sites in eastern Ottawa, but there were no significant differences in forest or wetland cover for all radii (Table 3).

TABLE 1. Land use surrounding sites with Boreal Chorus Frogs (*Pseudacris maculata*) in eastern Ottawa (n = 5) and western Ottawa (n = 42) at 0.5-, 1.0-, 1.5-, and 2.0-km radii. Median percentages were compared using the non-parametric Mann-Whitney test (W). Numbers in bold indicate a significant difference between eastern and western occupied sites (P < 0.05).

Land use class	Radius (km)	Eastern Ottawa sites (median %)	Western Ottawa sites (median %)	W	P
Agriculture	0.5	67.4	45.0	954	0.0649
	1.0	**64.8**	**46.5**	948	0.0401
	1.5	**65.4**	**47.2**	932	0.0092
	2.0	**69.0**	**48.1**	922	0.0032
Forest	0.5	9.9	17.0	1061	0.0701
	1.0	**3.7**	**18.1**	1066	0.0473
	1.5	6.0	21.6	1064	0.0555
	2.0	**4.7**	**22.1**	1073	0.0261
Wetland	0.5	9.4	17.1	1061	0.0701
	1.0	11.2	18.6	1049	0.1623
	1.5	**9.7**	**19.6**	1067	0.0435
	2.0	**9.3**	**18.1**	1083	0.0102

TABLE 2. Land use surrounding apparently unoccupied sites in eastern Ottawa (n = 179) and sites with Boreal Chorus Frogs (*Pseudacris maculata*) in western Ottawa (n = 42) at 0.5-, 1.0-, 1.5-, and 2.0-km radii. Median percentages were compared using the non-parametric Mann-Whitney test (W). Numbers in bold indicate a significant difference between apparently unoccupied eastern and occupied western sites (P < 0.05).

Land use class	Radius (km)	Unoccupied sites in eastern Ottawa (median %)	Occupied sites in western Ottawa (median %)	W	P
Agriculture	0.5	52.9	45.0	20469	0.1079
	1.0	54.5	46.5	20346	0.2014
	1.5	52.5	47.2	20488	0.0972
	2.0	**50.8**	**48.1**	20606	0.0483
Forest	0.5	14.0	17.0	19413	0.2219
	1.0	17.5	18.1	19507	0.3324
	1.5	17.0	21.6	19316	0.1385
	2.0	17.1	22.1	19203	0.0743
Wetland	0.5	**11.1**	**17.1**	18951	0.0139
	1.0	**13.0**	**18.6**	18975	0.0166
	1.5	**14.3**	**19.6**	18812	0.0046
	2.0	**16.0**	**18.1**	18790	0.0038

TABLE 3. Land use surrounding sites in eastern Ottawa with (n = 5) and apparently without (n = 179) Boreal Chorus Frogs (*Pseudacris maculata*) at 0.5-, 1.0-, 1.5-, and 2.0-km radii. Median percentages were compared using the non-parametric Mann-Whitney test (W). Numbers in bold indicate a significant difference between occupied and unoccupied sites (P < 0.05).

Land use class	Radius (km)	Occupied sites (median %)	Unoccupied sites (median %)	W	P
Agriculture	0.5	67.4	52.9	16448	0.3534
	1.0	64.8	54.5	16407	0.2016
	1.5	65.4	52.5	16371	0.1133
	2.0	**69.0**	**50.8**	16320	0.0436
Forest	0.5	9.9	14.0	16698	0.2333
	1.0	3.7	17.5	16720	0.1679
	1.5	6.0	17.0	16711	0.1927
	2.0	4.7	17.1	16742	0.1172
Wetland	0.5	9.4	11.1	16655	0.4089
	1.0	11.2	13.0	16628	0.5512
	1.5	9.7	14.3	16669	0.3447
	2.0	9.3	16.0	16745	0.1114

Discussion

Our surveys indicate that the Boreal Chorus Frog is rare in eastern Ottawa, and a decline seems to have occurred since the 1950s. Although our surveys undoubtedly failed to detect some populations, our survey technique has proven successful in the past. Using this technique, we found 30 previously undocumented Boreal Chorus Frog locations in western Ottawa (Seburn and Gunson 2011). One limitation of our survey technique is that auditory surveys were largely limited to wetlands visible from roads, and Boreal Chorus Frog populations may persist away from roads. However, only about 27% of the study area is more than 500 m from a road, the approximate distance at which a chorus can be heard.

Six broad classes of threats have been identified as causes of amphibian declines: commercial use (i.e., collecting), introduced/exotic species, land use change, contaminants, climate change, and infectious diseases (Collins and Crump 2009). Commercial use can be ruled out because the Boreal Chorus Frog is too small to be easily collected by humans. It is also unlikely that exotic species have caused the decline. Although introduced plants such as Purple Loosestrife (*Lythrum salicaria*) and European Common Reed (*Phragmites australis* ssp. *australis*) have altered wetlands, they are common across all of eastern Ontario including areas where the Boreal Chorus Frog remains widespread. The metabolite emodin from the invasive European Buckthorn (*Rhamnus cathartica*) can cause mortality of Boreal Chorus Frog embryos (Sacerdote and King, *in press*), but this shrub appears common in both eastern and western Ottawa (Soper and Heimburger 1985). It also seems unlikely that climate change would cause Boreal Chorus Frogs to decline in eastern Ottawa but not nearby in western Ottawa. This leaves three broad classes of threats: contaminants, infectious disease, or land use change.

Contaminants can be lethal to the Boreal Chorus Frog. Exposure to low levels (700 ppb) of the glyphosate herbicide Roundup WeatherMax (Monsanto Canada Inc., Winnipeg, Manitoba) resulted in 80% mortality of Boreal Chorus Frog tadpoles (Williams and Semlitsch 2010). The high mortality rate is likely a result of the unique surfactant in the product, as Roundup Original (Monsanto Canada Inc.) did not cause high levels of mortality (Williams and Semlitsch 2010). However, Roundup WeatherMax was not available in Canada until the early 2000s, and the Boreal Chorus Frog was declining before that (e.g., Daigle 1997), so it likely does not explain the declines. Nitrate contamination of surface waters from nitrogen-based fertilizers can also cause significant mortality of Western Chorus Frog tadpoles at levels of 10 mg/L or more (Hecnar 1995), but surface water data from the City of Ottawa suggest that nitrate levels are consistently below 10 mg/L, although it is possible they were higher in the past.

Infectious disease is another possibility. The chytrid fungus *Batrachochytrium dendrobatidis* has been detected in over 50 countries and over 500 species of amphibians (Olson *et al.* 2013). Infection can lead to chytridiomycosis, a fatal disease implicated in the decline of over 200 amphibian species (Fisher *et al.* 2009). The fungus has been detected in Boreal Chorus Frogs in southern Quebec, but no increased mortality or morbidity of frogs was observed (Ouellet *et al.* 2005). Thus, although chytridiomycosis cannot be excluded, again it is unlikely that it would affect frogs in eastern Ottawa but not western Ottawa.

Given that land use change resulting in habitat destruction is the leading cause of amphibian decline (Collins and Crump 2009; Collins 2010), it seems plausible that habitat loss is a prime driver of the decline in the Boreal Chorus Frog. The fact that unoccupied sites in eastern Ottawa had significantly lower wetland cover values at all spatial scales compared with occupied sites in western Ottawa (Table 2) suggests that landscape differences could explain the apparent decline; however, we have no direct evidence that wetland cover in eastern Ottawa has been reduced since the 1950s. One problem with this hypothesis is that occupied sites in eastern Ottawa did not differ in wet-

land cover from apparently unoccupied sites in eastern Ottawa (Table 3). Local conditions, such as hydrology, wetland configuration or connectivity, and the number of wetlands too small to be detected by our analyses, could explain the localized persistence of Boreal Chorus Frogs at occupied sites in eastern Ottawa. Wetland cover in all of Ottawa-Carleton declined from an estimated 47.2% circa 1800 to an estimated 13.2% in 1967, but no significant change in wetland cover occurred from 1967 to 2002 (Ducks Unlimited 2010*). Intensive farming practices in the 1950s and 1960s likely resulted in wetland loss, although we cannot document the extent of any loss.

The Boreal Chorus Frog is a short-lived frog, with more than 90% of adults breeding only once (Whiting 2004). Individuals typically remain within 275 m of breeding ponds (Desroches *et al.* 2001*) and wetland occupancy is correlated with the number of neighbouring occupied wetlands (Scherer *et al.* 2012). In the closely related Western Chorus Frog, stochastic events, such as premature drying of breeding ponds, can lead to annual extinction rates exceeding 50% (Werner *et al.* 2009). In addition, dry summers may limit successful immigration of Boreal Chorus Frogs to unoccupied wetlands (Schueler and Karstad 2013*). These factors suggest that wetland connectivity is important in ensuring that re-colonization can occur from neighbouring populations. Such lack of connectivity appears to be a factor in western Ottawa where isolated populations are more apt to become extirpated (Seburn and Gunson 2011).

Boreal Chorus Frogs likely persist across the landscape as a metapopulation (e.g., Gill 1978). If reduced wetland cover results in fewer wetlands, then it is plausible that wetland connectivity is reduced in eastern Ottawa. For example, a simulation of the loss of small wetlands in Maine demonstrated that this would result in a loss of total wetland area of 19%, but increase the inter-wetland distance by 67% (Gibbs 1993). Whether wetland connectivity has been reduced in eastern Ottawa cannot be explicitly tested using SOLRIS data, as wetlands smaller than 0.5 ha cannot be identified (OMNR 2007*). A detailed examination of wetland distribution and abundance in eastern and western Ottawa is required to determine whether wetland connectivity could explain the apparent decline of the Boreal Chorus Frog.

The most similar species that co-occurs with the Boreal Chorus Frog is the congeneric Spring Peeper (*Pseudacris crucifer*), which remains widespread in eastern Ottawa (DS, personal observation). Why should one species decline and the other remain widespread? In general, the closely related Western Chorus Frog is more common in ephemeral sites that tend to lack aquatic predators, whereas the Spring Peeper is more common in less ephemeral sites with more abundant aquatic predators (Skelly 1996). This also appears to be the case for the Boreal Chorus Frog in eastern Ontario (DS, personal observation). Small, ephemeral wetlands are often first lost when cropland expands and the result could be a landscape more suited to Spring Peepers than Boreal Chorus Frogs.

There is compelling evidence that the Boreal Chorus Frog has declined across much of eastern Ottawa and western Prescott and Russell. The lack of wetland cover in eastern Ottawa may have contributed to this decline, although additional research on abundance and distribution of small wetlands is required. Finding explanations for the widespread persistence of western Ottawa populations may also provide guidance for the conservation of this species.

Acknowledgements

Mike Oldham of the Natural Heritage Information Centre of the Ontario Ministry of Natural Resources graciously provided data from the Ontario Herpetofaunal Atlas. We thank Garnet Hanes for the data and maps from the surveys he conducted with the late Anne Hanes. Funding was provided by the Canadian Wildlife Federation. This paper benefited from review comments from Carolyn Seburn and four anonymous reviewers.

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Received 1 November 2013
Accepted 15 December 2013

Activity and Diet of Bats in Conventional versus Organic Apple Orchards in Southern Michigan

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Long, Brenna L., and Allen Kurta. 2014. Activity and diet of bats in conventional versus organic apple orchards in southern Michigan. Canadian Field-Naturalist 128(2): 158–164.

Organic farming practices have been suggested as a conservation strategy that can provide productive foraging sites for insectivorous bats in agricultural areas. We tested the hypothesis that the number and diversity of insects captured and the resulting activity and diet of bats would differ between organic and conventional apple orchards. During the summer of 2009 and 2010, we captured 131 Big Brown Bats (*Eptesicus fuscus*) and five Eastern Red Bats (*Lasiurus borealis*) by mist netting in four organic and four conventional orchards in Michigan. Acoustic monitoring revealed that most calls (59%) were produced by Big Brown Bats, followed by Hoary Bats (*L. cinereus*), Eastern Red Bats, and unidentified species of *Myotis*. Most insects (96%) captured in light traps were Coleoptera, Diptera, Hemiptera, Lepidoptera, and Trichoptera; fecal analysis indicated that Coleoptera dominated the diet of Big Brown Bats (79% by volume), followed by Diptera (14%). There were no significant differences between organic and conventional orchards in number of insects captured with light traps, bats captured with mist nets, acoustic recordings of bats, or proportion of Coleoptera and Diptera consumed by the bats. However, the taxonomic composition of captured insects and acoustic recordings was not homogenous among orchards in either group, suggesting that factors other than farming practices were more important in determining which insects and bats were found in the small orchards typical of southern Michigan.

Key Words: Big Brown Bat; *Eptesicus fuscus*; Eastern Red Bat; *Lasiurus borealis*; Hoary Bat; *Lasiurus cinereus*; bat activity; bat diet; apple orchard; organic farming; pesticides; Michigan

Introduction

Use of synthetic pesticides in conventional agriculture not only causes health concerns, but also incurs social and environmental costs (Cleveland *et al.* 2006). Although pesticides are helpful in controlling injurious species, such compounds can have a negative impact on beneficial organisms (Morales 2002). In addition, regular application of synthetic pesticides can result in a community of insects more resistant to specific chemicals (Turgut *et al.* 2011) and a need to develop new substances or apply more of the old, thus increasing production costs (do Amarante *et al.* 2008). A growing concern of both consumers and farmers over the use of pesticides has led some growers to move from conventional to organic practices (Meisterling *et al.* 2009; Turgut *et al.* 2011). Organic management excludes the use of synthetic pesticides and fertilizers, fungicidal and insecticidal soaps, botanical insecticides, and sulfur and copper compounds (Holb *et al.* 2003; Peck *et al.* 2006).

Differences in farming practices between organic and conventional farms should lead to differences in their communities of insects in terms of number of individuals, taxonomic composition, or both (Letourneau and Goldstein 2001; Bengtsson *et al.* 2005; Miñarro *et al.* 2009; Padmavathy and Poyyamoli 2011; Mates *et al.*, 2012). These presumed differences in insect communities should be reflected in the level of activity and diet of bats, the primary nocturnal predators on insects (Genghini *et al.* 2006; Braun de Torres 2011). In the United Kingdom, for example, Wickramasinghe *et al.* (2003) claimed that organic farms provided islands of high-quality foraging habitat for insectivorous bats and proposed organic practices as a potential tool for increasing the numbers and kinds of bats in agricultural areas.

In this study, we tested the hypothesis that organic procedures affect the number and diversity of bats and insects in orchards that grow apples, an economically important crop in Canada and the United States (Ontario Ministry of Agriculture and Food 2007*; USDA 2012*). We predicted that the abundance and diversity of both bats and insects would be greater at organic sites. Based on the presumed greater abundance of insects on organic farms, we also predicted that reproductively active adult female bats, which must bear the high energetic cost of pregnancy and lactation (Kurta *et al.* 1989, 1990), would be more common in organic orchards, relative to adult males and non-reproductive females, than at conventional sites. Finally, many species of bats are selective opportunists, generally concentrating on certain types of prey but often increasing consumption of locally abundant taxa (Fenton and Morris 1976; Murray and Kurta 2002). Consequently, we predicted that the diet of bats would vary between organic and conventional sites, reflecting the assumed differences in composition of the insect community.

Study Area

Our study took place in four organic and four conventional apple orchards in southern Michigan, within 200 km of Jackson (41°51' to 43°1'48"N, 83°40'12" to

84°51'36"W; Smith 2012). All orchards were in rural, agricultural areas, with corn and soy as the most common crops. The apple trees in the eight orchards were either small dwarf varieties (1–3 m in height) or semi-dwarf trees (3–5 m in height). Orchards varied in size from 5.7 to 24.3 ha, with a mean of 13.2 ha. Average distance between an orchard and the closest other orchard used in the study was 112 km ± 10 (SE). All fieldwork took place between 5 June and 13 August 2009 and between 18 May and 12 August 2010.

Methods

Field and laboratory techniques

To sample insects, we used a light trap (Model 2815A, BioQuip, Gardena, California), powered by a 12-volt battery. Light trapping occurred at only one orchard on any given night and coincided with mist netting for bats (see below). The trap was turned on 1 h before sunset and deactivated about 5 h later, immediately after the mist-netting system was dismantled. Captured insects were preserved in 70% ethanol for later counting and identification to order with the aid of a dissecting microscope.

Bats were captured using mist nets made from 50-denier, braided nylon (Avinet, Dryden, New York). Netting systems were 6–9 m high and 6–12 m wide, depending on the size of available flight corridors. Mist netting was typically carried out 3–5 times a week, depending on weather, but in only one orchard on any given night. Netting began at sundown and continued for 4 h. Ambient temperature was recorded at the beginning and end of mist netting. Each captured bat was identified to species, sexed, and classified as adult or juvenile, depending on fusion of the epiphyseal plates at the metacarpal-phalangeal joints (Anthony 1988). Females were further identified as non-reproductive, pregnant, lactating, or post-lactating based on body mass, abdominal palpation, and ability to express milk from the nipples (Racey 1988).

Fecal samples were collected from each captured bat by placing the animal in a paper lunch bag until defecation occurred. Fecal pellets were frozen for later examination, when each pellet was soaked in 95% ethanol and teased apart under a dissecting microscope. The resulting insect fragments were identified to order, and the percent volume of each order was estimated visually for each pellet (Whitaker 1988).

To complement mist netting, we used ultrasonic detectors to assess activity of bats. Each monitoring unit consisted of an ultrasonic detector (Anabat II, Titley Electronics, Ballina, Australia), a zero-crossings analysis interface module (ZCAIM), and a small battery (12-volt, 5 A-h) housed in a protective case. A 5-cm diameter opening was cut into the side of the case, and a piece of polyvinylchloride pipe in the shape of a flat U was attached (Smith 2012). When in use, the microphone of the detector rested inside the inner opening of the pipe. The detector sensed ultrasound produced by each bat, whereas the ZCAIM transformed the sound into a digital signal and recorded the frequency-versus-time structure of the call as a file on a compact flash card inside the ZCAIM. Detectors were calibrated against each other before use (Larson and Hayes 2000) with an ultrasonic distance-measuring device (Model 10065, Sonin, Charlotte, North Carolina).

Eight monitoring units were established, one at each orchard. Each unit was programmed to record from about 30 minutes before local sunset to about 30 minutes after local sunrise. During recording, the cases were positioned on a pole, about 6 m above the ground. After downloading files each week, we moved the unit to a new, randomly selected site in each orchard.

The number of files recorded per night was used as a measure of bat activity. If a particular monitoring unit did not function for the entire night, then all results from that night were discarded. Recorded calls were examined using Analook W software (version 3.3q, 2006, http://hoarybat.com) and assigned to one of four groups: *Myotis* spp., Eastern Red Bat (*Lasiurus borealis*), Hoary Bat (*Lasiurus cinereus*), or Big Brown Bat (*Eptesicus fuscus*) (Flaquer *et al.* 2007; Brooks 2009; Morris *et al.* 2010). Although a few calls categorized as Big Brown Bat may have been made by Silver-haired Bats (*Lasionycteris noctivagans*), the latter species is rare, representing less than 0.1% of bats that are mist netted in southern lower Michigan in summer (Winhold and Kurta 2008; Kurta 2010). No attempt was made to categorize sequences of calls with fewer than three individual pulses or consisting of pulses of low quality (Johnson *et al.* 2002; Francl 2008; Johnson and Gates 2008).

Statistical analyses

We focused our analysis on Big Brown Bats because they were the predominant species in the area. To determine differences in diet between the two types of orchards, we used two-sample independent *t*-tests. Chi-squared tests were used to examine differences in the composition of insects (by order) captured and differences in calls of bats recorded at the two types of orchards. In addition, chi-squared tests were used to analyze differences between the two types of orchards in terms of the proportion of reproductive versus non-reproductive female Big Brown Bats and male versus female adult Big Brown Bats. Both types of tests were conducted using VassarStats (Lowry 2008*).

A nested analysis of variance was used to detect differences between organic and conventional orchards in the number of acoustic records, bats netted, and insects captured. Only orders of insects that contributed at least 5% of the total amount captured were included in the comparison. Minimum ambient temperature was used as a covariate in these three analyses, because temperature can affect the number and diversity of insects that are active (e.g., see Ciechanowski *et al.* 2007; Le Lann *et al.* 2011). To obtain normally distributed data, we added 1 to the raw counts obtained from

acoustic monitoring, mist netting, and light trapping and applied a logarithmic transformation before performing statistical analyses. Analyses were performed primarily with Systat 10.2 (Systat Software, Inc., Richmond, California) or Excel (Microsoft, Redmond, Washington).

A nested analysis of variance was also used to compare the percent volume of various orders of insects found in the diet of bats from organic and conventional orchards. The percent volume represented by each insect order in the fecal pellets produced by each bat was converted to a proportion, and the square root of each proportion was arcsine-transformed to attain normal distribution of the data (Zar 1999). Only orders that contributed at least 5% of the total volume were included in these comparisons.

Different practices in conventional and organic orchards could affect not only the overall level of activity of bats and insects, but also the structure of the local communities (Bengtsson *et al.* 2005; Macfadyen *et al.* 2009; Power and Stout 2011). Consequently, we also calculated taxonomic diversity, using the level of species or genus for the bats and order for the insects that were captured or identified in the feces. As a measure of diversity, we used Simpson's index, which is equal to $1 - [\sum n_i(n_i - 1)] / N(N - 1)$, where n_i is the number of individuals in each taxonomic group and N is the total number of captured species or orders (Brower and Zar 1984). We calculated diversity for each orchard and compared mean diversity of organic and conventional orchards using a standard t-test. All data are presented as the mean and standard error (SE), and alpha was set to 0.05 for all statistical tests.

Results

Over the 2 years of our study, we trapped insects on 36 nights in organic sites and 38 nights in conventional orchards for a total of 5233 insects (138 ± 22 insects/night) from the organic orchards and 4179 insects (116 ± 20 insects/night) from conventional orchards. There was no significant difference between the two types of orchards in number of insects trapped per night ($F_{1,6} = 0.03$, $P = 0.87$). Five orders of insects — Coleoptera (beetles), Diptera (flies), Hemiptera (true bugs), Lepidoptera (moths), and Trichoptera (caddisflies) — accounted for 96% of the insects captured. There was no significant difference between the two types of orchards in numbers of insects by order captured per night (all $F_{1,6} \leq 0.54$, $P \geq 0.49$; Table 1). The mean diversity at the ordinal level was also not significantly different ($t_{3.2} = 1.95$; $P = 0.13$): organic locations (0.71 ± 0.03) and conventional orchards (0.76 ± 0.00).

Beetles were the most abundant order of insects in both types of orchard, representing 40% and 31% of captures in organic and conventional orchards, respectively (Table 1). The next most common order at organic sites was moths (21%), but at conventional orchards flies were the second most abundant order (23%). A preliminary chi-squared test indicated significant heterogeneity in the composition of the five most common orders of insects among both the organic ($\chi^2_{12} = 293.57$; $P < 0.001$) and conventional ($\chi^2_{12} = 615.74$; $P < 0.001$) orchards, which precluded a statistically valid comparison of the overall composition of insects between types of orchards using chi squared.

Mist netting was carried out on 37 nights in organic and 38 nights in conventional apple orchards and yielded 136 bats. Of these bats, 54 (39.7%) were netted in organic orchards (1.5 ± 0.4 captures/night), and 82 (60.3%) in conventional orchards (2.2 ± 0.6 captures/night). The difference in number of captures per night between organic and conventional orchards was not significant ($F_{1,6} = 0.26$, $P = 0.63$).

We caught 131 Big Brown Bats and 5 Eastern Red Bats — the two most common species in the region (Winhold and Kurta 2008; Smith 2012) — and we focus our analyses on the more-abundant Big Brown Bat. They consisted of 44 adult females, 27 juvenile females, 32 adult males, and 28 juvenile males. Of the adult females, 14 reproductive (six pregnant, three lac-

TABLE 1. Average number (%) of insects of the five most abundant orders captured per night at each orchard in southern Michigan. Orders contributing less than 5% of the total number of insects trapped in both types of orchard were not included (Smith, 2012); thus, row percentages do not total 100%.

Orchard	Lepidoptera	Coleoptera	Diptera	Hemiptera	Trichoptera	Total
Orchard						
AlMar E	3.6 (17.4)	8.9 (42.7)	5.3 (25.2)	0.5 (2.4)	2.5 (12.1)	20.8 (99.8)
AlMar SE	6.1 (18.7)	11.8 (36.0)	6.2 (19.0)	4.3 (13.2)	4.1 (12.7)	32.5 (99.6)
Apple Schram	11.4 (32.1)	15.2 (42.7)	3.8 (10.8)	1.9 (5.5)	2.9 (8.3)	35.2 (99.4)
Country Mill	3.4 (12.8)	10.9 (40.6)	5.3 (19.6)	2.8 (10.5)	4.3 (15.9)	26.7 (99.4)
Total	24.6 (21.2)	46.8 (40.3)	20.6 (17.7)	9.6 (8.3)	13.9 (12.0)	115.5 (99.5)
Conventional						
Erwin	5.1 (18.4)	9.8 (35.6)	4.4 (15.9)	1.3 (4.6)	6.8 (24.6)	27.4 (99.1)
Spicer	4.6 (25.3)	5.9 (32.3)	3.8 (20.7)	1.9 (10.6)	1.9 (10.5)	18.1 (99.4)
Swinderman N	3.3 (5.0)	18.5 (27.9)	19.6 (29.5)	2.7 (4.1)	20.2 (30.6)	64.3 (97.1)
Swinderman S	2.9 (11.3)	8.9 (34.8)	4.1 (16.1)	1.2 (4.7)	1.2 (4.7)	18.3 (71.6)
Total	15.9 (11.6)	43.1 (31.3)	31.8 (23.1)	7.1 (5.2)	30.1 (21.8)	128.0 (93.0)
Overall average	20.1 (15.9)	44.9 (35.3)	26.4 (20.7)	8.3 (6.5)	22.2 (17.5)	121.9 (95.9)

tating, and five post-lactating) and 3 non-reproductive bats were netted in organic orchards and 21 reproductive (4 pregnant, 13 lactating, and 4 post-lactating) and 6 non-reproductive bats were netted in conventional orchards. The difference in proportion of reproductive and non-reproductive female Big Brown Bats between organic and conventional orchards was not significant ($\chi^2_1 = 0.0$; $P = 1$). The ratios of male to female adults (15:17 in organic orchards and 17:27 in conventional orchards) were also not significantly different ($\chi^2_1 = 0.23$; $P = 0.63$).

Acoustic monitoring records for the combined field seasons consisted of 25 945 files containing sounds made by bats during 569 detector-nights; a detector-night was defined as a complete night of recording, from before sunset to after sunrise, by one detector. Of these files, 10 217 were recorded on 279 detector-nights in the four organic orchards, whereas 15 728 were recorded on 329 detector-nights in the four conventional orchards. Although more files per night were recorded in conventional orchards (51 ± 14 files/night) than in organic orchards (37 ± 8 files/night), the difference was not significant ($F_{1,6} = 0.20$, $P = 0.67$).

We assigned 11 045 (43%) of the recordings to genus or species. Most calls from all orchards were produced by Big Brown Bats (59%), followed by Hoary Bats (28%), Eastern Red Bats (13%), and *Myotis* spp. (< 1%; Table 2). The mean diversity of bats in organic orchards (0.53 ± 0.02) was not statistically different ($t_6 = 0.78$; $P = 0.23$) from that in conventional orchards (0.57 ± 0.05). A preliminary chi-squared test indicated considerable heterogeneity in taxonomic composition of the calls of bats in both organic ($\chi^2_9 = 109$; $P < 0.001$) and conventional ($\chi^2_9 = 424$; $P < 0.001$) orchards, which prevented a statistically meaningful comparison of overall composition between the two types of orchards using chi squared.

We examined 131 fecal pellets from Big Brown Bats and found that, overall, their diet included five orders of insects: Coleoptera (79.3% by volume), Diptera (13.2%), Lepidoptera (0.6%), Hemiptera (0.7%), and Hymenoptera (0.7%; Table 3). Mean diversity of the diet at the ordinal level was not significantly different ($t_6 = 0.95$; $P = 0.19$) between organic locations (0.30 ± 0.04) and conventional orchards (0.36 ± 0.05). There were no significant differences between organic and conventional orchards in percentage volume of the two most common orders: Coleoptera ($F_{1,6} = 0.21$, $P = 0.66$) and Diptera ($F_{1,6} = 0.01$, $P = 0.92$).

TABLE 2. Numbers (and %) of bats identified from recordings by ultrasonic detectors in four organic and four conventional apple orchards in southern Michigan.

Species	Organic orchard	Conventional orchard	Total
Big Brown Bat	2943 (63.7)	3554 (55.3)	6497 (58.8)
Hoary Bat	1030 (22.3)	2030 (31.6)	3060 (27.7)
Eastern Red Bat	631 (13.7)	826 (12.9)	1457 (13.2)
Myotis spp.	15 (0.3)	16 (0.3)	31 (0.3)
Total	4619	6426	11 045

Note: Big Brown Bat, *Eptesicus fuscus*; Hoary Bat, *Lasiurus cinereus*; Eastern Red Bat, *L. borealis*.

TABLE 3. Percent volume of insects, by order, consumed by Big Brown Bats, *Eptesicus fuscus*, in four organic and four conventional apple orchards in southern Michigan based on fecal pellet analysis. Columns may not add to 100 because of rounding errors.

	Volume consumed (%)		
Insect order	Organic orchard (n = 52 bats)	Conventional orchard (n = 79 bats)	Total (n = 131 bats)
Coleoptera	79.3	78.0	78.6
Diptera	13.2	13.9	13.5
Lepidoptera	0.6	1.3	1.0
Hemiptera	0.7	1.1	0.9
Hymenoptera	0.7	0.2	0.5
Unknown	5.5	4.5	5.0

Discussion

We predicted that adult female bats would be more common in organic orchards than conventional ones, but the sex ratio of adult Big Brown Bats did not differ between types of orchard, nor did the ratio of reproductive to non-reproductive adult females. Although our predictions were not upheld, this is not surprising because they were predicated on an assumed difference in the insect community between organic and conventional orchards. However, light trapping revealed that total abundance and diversity of insects, as well as the abundance of the five most common orders of insects, did not differ between types of orchards (Table 1). Availability of prey at the ordinal level, therefore, was

similar in organic and conventional apple orchards, suggesting no reason for energetically stressed females to favour one type of orchard over the other.

To date, only one quantitative study has been published concerning activity of bats on organic and conventional farms of any type (Wickramasinghe *et al.* 2003). The authors compared bat activity on organic and conventional farms in England and Wales, using acoustic monitoring and captures via mist net, as we did in Michigan. However, they reported that bat activity was 61% greater on organic than conventional farms. Also, in a companion study, Wickramasinghe *et al.* (2004) detected a significantly greater number of insects belonging to five families at organic locations, although pairwise statistical comparisons of 13 other families showed no differences between organic and conventional sites.

However, the farms in the studies by Wickramasinghe *et al.* (2003, 2004) differed greatly from ours. Fifty-four percent of the farms in Wickramasinghe *et al.* (2004) were classified as livestock operations and another 41% were mixed, involving both livestock and unspecified crops. The farming practices and potential chemicals used in pastures and orchards differed. For example, avermectin, an antihelminthic drug often used with cattle and sheep on conventional farms, can reduce the number of invertebrates using ungulate feces, i.e., dung beetles (Scarabaeidae and Geotrupidae; Strong 1992), which are commonly eaten by some British bats (Wickramasinghe *et al.* 2004). Furthermore, Wickramasinghe *et al.* (2003, 2004) sampled bats and insects in various habitats, and most differences they reported involved pastoral and aquatic habitats; these habitats generally were not present in the orchards we studied (Smith 2012). Finally, the average size of their farms (about 51 ha; Wickramasinghe *et al.* 2003) was more than double the area of our largest orchard (24 ha).

Wickramasinghe *et al.* (2003) proposed organic practices as a potential conservation strategy for increasing the numbers and kinds of bats in agricultural regions. However, we were unable to document differences in the number, richness, and diversity of bats; in the dietary composition of the bats; in overall activity and diversity of insects at the ordinal level; or in the abundance of particular orders of insects. The fact that taxonomic composition of the captured insects and the acoustic recordings of bats were not homogenous among either conventional or organic orchards suggests that factors other than farming practices, such as differing patterns of land use and habitats in the surrounding landscape, were more important in determining the types of insects and bats found in apple orchards typical of southern Michigan.

Apple orchards in other parts of North America, though, can be as large as 1200 ha (Washington Apple Commission 2010*), and a suggested area of further study is to examine the relation between size of orchard and potential differences in their associated communities of insects and bats. Large size might insulate the interior of organic orchards from surrounding conventional farms and potentially allow development of disparate communities, as found by Wickramasinghe *et al.* (2003, 2004). In addition, recent advances in molecular techniques, such as high-throughput sequencing (Bohmann *et al.* 2011; Razgour *et al.* 2011), now allow biologists to sequence the DNA of every item of prey in the fecal material produced by a bat. Although many sequences obtained in this manner cannot be identified to species or other taxonomic level below order, use of molecular operational taxonomic units offers a promising way of comparing diversity of prey in different types of orchards at a more detailed level than visual analysis (Chesters *et al.* 2013; Rolfe *et al. in press*). Further research, concerning organic practices and bats is warranted, because bats are experiencing unprecedented mortality in North America from wind turbines (Kunz *et al.* 2007) and white-nose syndrome (Turner *et al.* 2011), and determining factors that promote the conservation of these flying mammals is essential to their long-term survival.

Acknowledgements

We thank the farmers and their assistants for providing access to their orchards: J. Bush (Apple Schram Orchard), B. Erwin (Erwin Orchard), J. Koan (AlMar Orchard), A. Spicer (Spicer Orchard), J. Swinderman (Apple Wood Orchard), and S. Tennes (Country Mill Orchard). S. Francoeur and C. Rockey provided advice on statistics and acoustic monitoring, respectively. We thank Mckinley Ophelia for keeping BLL company on many long nights in the orchards when everyone else was asleep. A. Rolfe and J. Veilleux provided helpful comments on the manuscript. Financial support was provided by a grant from the Organic Farming Research Foundation to S. Tennes; a Faculty Research Fellowship from Eastern Michigan University awarded to AK; and a Hellwig Research Award given to BLL by the Department of Biology at Eastern Michigan University.

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Received 8 November 2013
Accepted 28 January 2014

Decline in Breeding of the Great Black-backed Gull, *Larus marinus*, and the Herring Gull, *L. argentatus*, on Boot Island, Nova Scotia, 1986 to 2010

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MacKinnon, Colin M., and Andrew C. Kennedy. 2014. Decline in breeding of the Great Black-backed Gull, *Larus marinus*, and the Herring Gull, *L. argentatus*, on Boot Island, Nova Scotia, 1986 to 2010. Canadian Field-Naturalist 128(2): 165–172.

For over 50 years, Boot Island, Nova Scotia, has supported a significant mixed bird colony: Great Black-backed Gull (*Larus marinus*), Herring Gull (*L. argentatus*), Great Blue Heron (*Ardea herodias*), and Double-crested Cormorant (*Phalacrocorax auritus*). In 2002, the largest Great Black-backed Gull colony in Canada was located there. Over the last quarter century, the Herring Gull colony has shown a dramatic and near-linear decrease from 727 nests in 1986 to 67 in 2000; in 2010, only two nests remained. The number of Great Black-backed Gull nests has also declined by 44%, from 1467 nests in 1992 to 819 in 2010. These reductions may be partly attributed to factors external to the colony, such as changes in regional fisheries and better landfill management. However, a more immediate problem may be nest predation and disturbance by American Mink (*Neovison vison*), Raccoon (*Procyon lotor*), Coyote (*Canis latrans*), and Bald Eagle (*Haliaeetus leucocephalus*).

Key Words: Great Black-backed Gull; *Larus marinus*; Herring Gull; *Larus argentatus*; Boot Island; National Wildlife Area; Nova Scotia; nesting; population decline

Introduction

Following the indiscriminate slaughter of many seabirds in the late 19th and early 20th century, often for the millinery trade, Great Black-backed and Herring Gulls recovered with a dramatic increase in numbers, resulting in great overlap in their breeding ranges (Drury 1973). In the first half of the 20th century, Herring Gulls were by far the more numerous (Drury 1973). However, after reaching a peak in the 1970s and 1980s, their numbers along the east coast of North America started to decline, while Great Black-backed Gull numbers continued to increase (Brown *et al.* 2001 **in** Rome and Ellis 2004; Shoals Marine Laboratory 2010*). Currently, in eastern Canada, the Great Black-backed Gull is deemed "not currently at risk" while Herring Gull populations are of "moderate" concern as there is an apparent population decline (Milko *et al.* 2003*).

These colonial birds require remote, disturbance-free habitat in which to nest. The Great Black-backed Gull, *Larus marinus*, and the Herring Gull, *L. argentatus*, are ground-nesting birds that are highly susceptible to mammalian predation and, thus, seek out isolated breeding locations (Pierotti and Good 1994). Such colonies are frequently situated on remote islands where monitoring by counting the number of nests is often difficult because of poor and limited site access and a narrow survey window.

Surveys of Great Black-backed and Herring Gull colonies are conducted regularly in eastern Canada. However, when time and resources are limited, a trade-off is made between monitoring a few colonies intensively and conducting infrequent surveys of many colonies over a wide geographic area. Broad-scale surveys, frequently conducted from the air, predominate as the desired method of monitoring populations at a regional scale. However, aerial counts are not as accurate as ground surveys (Drury 1973; Boyne and Hudson 2002*) and are often of limited value in tracking population trends of individual colonies.

Gull colonies in Boot Island National Wildlife Area (Kings County, Nova Scotia) present a unique monitoring opportunity for eastern Canada because biennial surveys of colonial nesting birds have been undertaken as part of the National Wildlife Area's management regime since 1984. In this article, we assess changes in the size of both Great Black-backed and Herring Gull colonies from 1986 to 2010 and discuss possible factors affecting the multiyear decline in both species.

Study Area

Boot Island National Wildlife Area is located in the southern bight of Minas Basin at the mouth of the Gaspereau River, 8 km northeast of Wolfville, Kings County, Nova Scotia (45°08'N, 64°16'W). The 107-ha wildlife area consists of approximately 91 ha of salt marsh and 16 ha of uplands (Figure 1). The uplands comprise the 15.5-ha main island (2.0 ha forested and 13.5 ha of open habitat) as well as a 0.5-ha treeless and much smaller "Cyril's Island" (Little Boot Island). The upland portion of Boot Island slopes gently upward from the salt marsh in a northeast direction, such that the seaward face consists of an actively eroding 6-m high mud and sandstone cliff. The small forested area is dominated by a dense stand of dead and dying White

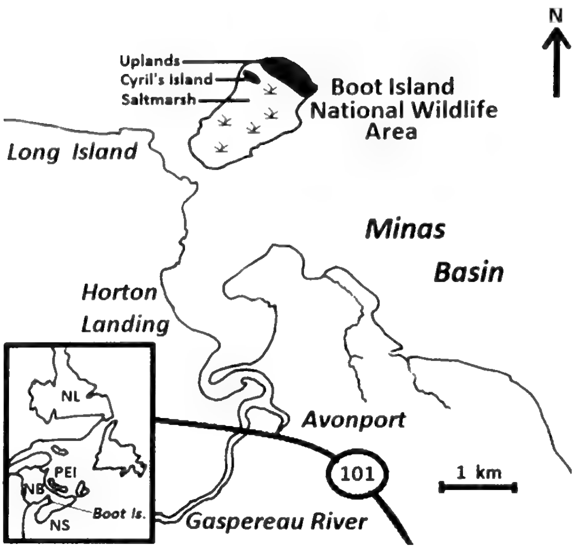

FIGURE 1. Location of Boot Island National Wildlife Area, Kings County, Nova Scotia.

Spruce (*Picea glauca*) with scattered Red Maple (*Acer rubrum*), Trembling Aspen (*Populus tremuloides*), and Balsam Fir (*Abies balsamea*). Decay of the forest has been exacerbated by the deleterious effects of tree-nesting Great Blue Herons (*Ardea herodias*) (see MacKinnon and Kennedy 2006*).

The area of open field habitat, where most Great Black-backed and Herring Gull nests are located, is dominated by two species of wild mustard: Wild Radish (*Raphanus raphanistrum*) and Hairypod Hedgemustard (*Sisymbrium officinale*). The remaining area is composed of open field and rough cover consisting of a nearly impenetrable thicket of Virginia Rose (*Rosa virginiana*), American Red Raspberry (*Rubus idaeus*) and Northern Bayberry (*Myrica pensylvanica*) (Newell *et al.* 2006*).

Historically, Boot Island supported large colonies of Great Black-backed and Herring Gulls. The island also supports a large colony of Great Blue Herons and Double-crested Cormorants (*Phalacrocorax auritus*), and once supported a significant winter roost of American Crows (*Corvus brachyrhynchos*) (Milton 1983). However, around 1991 the crows relocated 19.5 km to the southwest to the town of Kentville on the mainland. The inter-tidal mudflats in the vicinity of the island are recognized as a RAMSAR site (a wetland of international importance) and support a diversity of migrant shorebirds (Elliot 1977; Hicklin 1981, 1984; Mawhinney 1991*; Gilliland 1992). These flats also sustain a commercial bait (Bloodworm, *Glycera dibranchiata*) industry (Klawe and Dickie 1957*).

Until the late 1800s, Boot Island was connected to the mainland and it has a long history of human use (Mitcham 1986). The island was farmed intensively, and an extensive system of dykes and ditches draining the adjacent salt marshes existed until agricultural activities ceased in approximately the 1930s.

Over many decades, biologists and naturalists have visited Boot Island and reported wildlife observations. The late Cyril Coldwell, curator of Acadia University's ornithology collection, provided most colonial bird observations throughout the 1960s. The first detailed survey of colonial birds on Boot Island was carried out by Barkhouse (1976*), who also summarized past observations, reporting that gulls started nesting on the island around 1948 followed shortly after by breeding Great Blue Herons. Double-crested Cormorants were first reported nesting in 1967.

Methods

Between 1976 and 2010, 14 surveys of gull nests were completed, recording both occupied and unoccupied nests. All surveys were centred at the peak or the end of the Great Black-backed Gull's egg-laying period in mid-May (survey dates ranged from 8 to 19 May, average 13 May). Although Herring Gulls lay slightly later than Great Black-backed Gulls, full (three-egg) clutches of the former were frequently encountered, and thus we believe that this single survey window adequately captured the number of nests occupied by both species. Slight variations in survey date were due to weather and travel conditions, as the tidal waters between Boot Island and the mainland are extremely hazardous. No surveys were conducted during cold or wet conditions (see Diamond 2001*).

Following the census method described by Barkhouse (1976*), surveys were carried out by walking a series of parallel transects across the narrowest width of the colony. Observers walked abreast and within close proximity to each other. The outermost observers temporarily marked the flanks of each transect with red flagging tape. On completion of a transect, the group wheeled around in unison so that on the return transect, the person who had been on the outermost flank followed his or her previously marked line. One person in the centre, usually the crew leader, was the recorder. The crew leader set the transect width, based on observer visibility and nesting density and recorded and confirmed observations relayed from the rest of the team. Observations reported orally by crew members were repeated by the recorder for confirmation. The crew leader also kept track of crew observations visually to prevent duplication or missed nests. All movement within the colony was kept to a minimum. To reduce disturbance, hand signals were often used to relay instructions, such as change direction, stop, proceed, etc.

Contents of Great Black-backed and Herring Gull nests (empty, number of eggs and/or number of chicks) were recorded. Any structure more elaborate than a simple scrape with some built-up edge was deemed a nest (Diamond 2001*). To distinguish between Great Black-backed and Herring Gull eggs, the following criteria were used:

Locations of grouped Herring Gulls within the larger colony of Great Black-backed Gulls were noted.

The approximate position of individual Herring Gulls on nests in relation to adjacent features (bush, rock, etc.) was visually tracked.

The sizes of all eggs, in each nest, were visually attributed to species; Herring Gull eggs are about 19% smaller than Great Black-backed Gull eggs (Bent 1963*), although there is some variation in size between regions (see Pierotti and Good 1994; Good 1998). The collective size of all eggs in a specific nest, along with the above supporting criteria, were used to identify it as either Great Black-backed or Herring Gull.

A survey typically required 4–6 hours to complete. To minimize further disturbance within the gull colony and adjacent Great Blue Heron and Double-crested Cormorant colonies, nests were not marked to determine a correction factor (e.g., Lincoln index).

To test whether the population decline of gulls was significant, we used a linear regression analysis. The regression and regression equations were calculated using the statistical package within Microsoft Excel while t and P values were calculated as per Schefler (1980); applying the two-tailed test.

Results and Discussion

Herring Gull nests were first recorded in significant numbers in 1976 (712 nests; Figure 2). The number of nests peaked in 1986 (727 nests), but by 2010, only 2 nests were recorded in the survey. The near-linear decline in the number of Herring Gull nests on Boot Island from 1986 to 2000 suggests a constant pressure on these birds ($R^2 = 0.99$, $y = -46.394x + 92\,857$, $n = 7$ surveys, $t = 25.7$, $P < 0.01$) (Figure 2).

The number of Great Black-backed Gull nests were also first recorded in significant numbers in 1976 (N = 1005). The number of nests peaked in 1992 (N = 1467), and by 2010, the number of nests had decreased by 44% to 819. The decline of Great Black-backed Gull nests was significant but a more variable decline from 1992 to 2010 ($R^2 = 0.82$, $y = -31.434x + 64\,010$, $n = 9$ surveys, $t = 5.74$, $P < 0.01$) (Figure 2).

Although the survey window remained the same between 1976 and 2010, the ratio of occupied to unoccupied Great Black-backed Gull nests fell from a high of 22.3:1 in 1986 to just 2.3:1 in 2010 (Figure 3). While the Great Black-backed Gull colony was declining, there was a noted increase in the proportion of empty nests. This could be a result of young and inexperienced breeders nesting later, although we believe that the increase in empty nests reflects an increase in predation on eggs and/or chicks. For Herring Gulls, the ratio of occupied to empty nests ranged from 3.7:1 in 1986 to an average of 4.1:1 from 1996 to 2000 (Figure 4). The observed differences in the ratios may reflect both the timing of heavier predation and an artefact

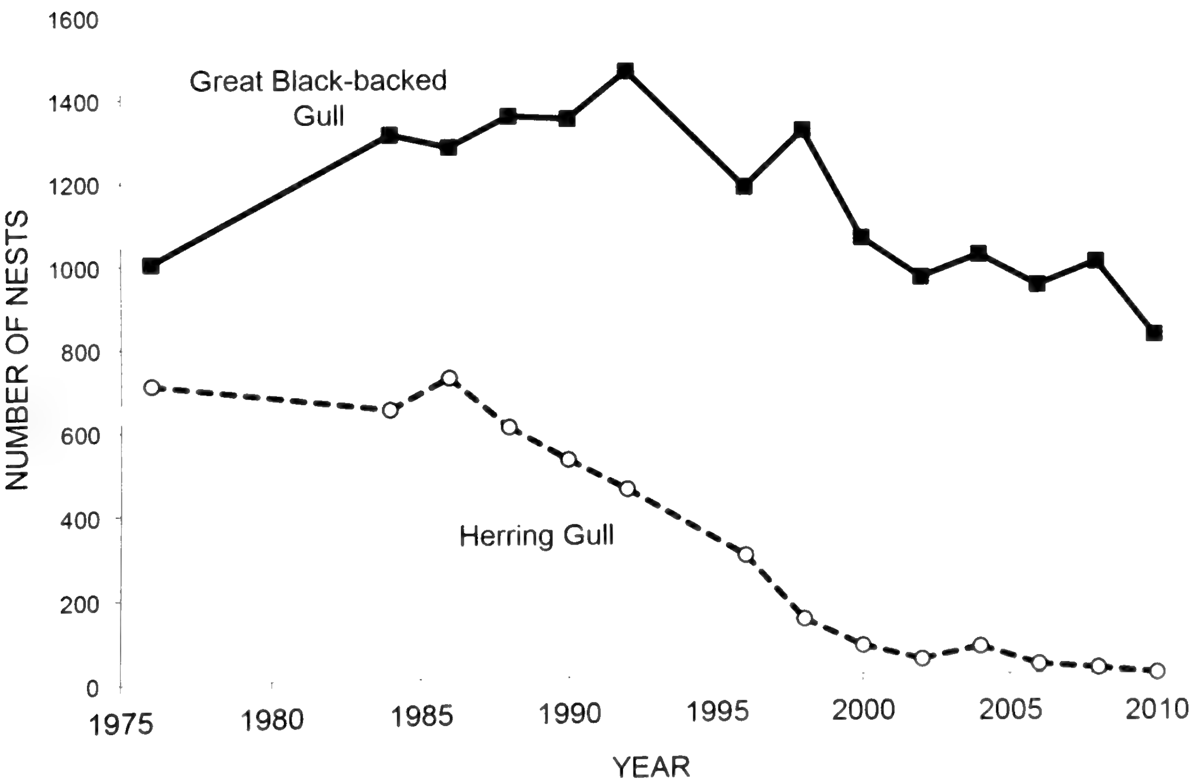

Figure 2. Number of nests (occupied and unoccupied) of Great Black-backed Gulls (*Larus marinus*) and Herring Gulls (*L. argentatus*) found at Boot Island National Wildlife Area, Nova Scotia, 1976 to 2010.

of the survey window, as Great Black-backed Gulls begin egg laying earlier than Herring Gulls. It is noteworthy that there was an increase in the ratio of occupied to empty Great Black-backed Gull nests from 2006 to 2010 when the Herring Gull colony had been reduced to fewer than 25 nests (Figures 3 and 4). During this same period, Coyote began to visit the island and predation by this species became a more obvious and regular event (MacKinnon *et al.* 2007).

It is well documented that Great Black-backed Gulls are more aggressive and may out-compete Herring Gulls as well as preying on young birds (Threlfall 1968; Rome and Ellis 2004; Cotton 2009). This may at least partly explain the earlier onset of the Herring Gull decline. However, by the early 1990s, both species were in decline and other factors must be considered.

During this period of decline in both gull species and the increasing proportion of empty Great Black-backed Gull nests, the breeding numbers in the adjacent Great Blue Heron and Double-crested Cormorant colonies remained relatively constant. From 1984 to 2010, Great Blue Herons and Double-crested Cormorants averaged 53 nests (range 38–75, $n = 13$ surveys) and 232 nests (range 147–351, $n = 13$ surveys), respectively (MacKinnon *et al.* 2010*). No obvious overall change or trend in colony size was observed. The factors influencing the gull decline are apparently not affecting the health of the adjacent tree-nesting colonial species.

It is worth noting that, based on 2002 aerial survey data (753 pairs), the Great Black-backed Gull colony on Boot Island, Nova Scotia, was the largest in Canada (Cotter *et al.* 2012*). Furthermore, if Herring Gulls were deserting Boot Island for other locations, currently the closest large Herring Gull colony is situated in an inland bog 195 km to the southwest on Briar Island, Nova Scotia. (Environment Canada 2008*; Cotter *et al.* 2012*).

Food Availability

Human refuse and landfills

Changes in the handling of human refuse, such as the closure or reduction of landfills, have been cited as one reason for decreases in gull populations (Drury 1973; Shoals Marine Laboratory 2010*). In Nova Scotia, a solid waste management strategy was released in 1995 (Friesen 2000), although organic garbage was not banned from the province's landfill sites until 30 November 1998 (Speed 2000*). By this time, the Herring Gull colony on Boot Island had already collapsed and Great Black-backed Gull numbers were in decline. Although competition for limited food resources may have been partly responsible for the changes in the colony, we do not have any direct evidence that the changes in management of human refuse in the vicinity

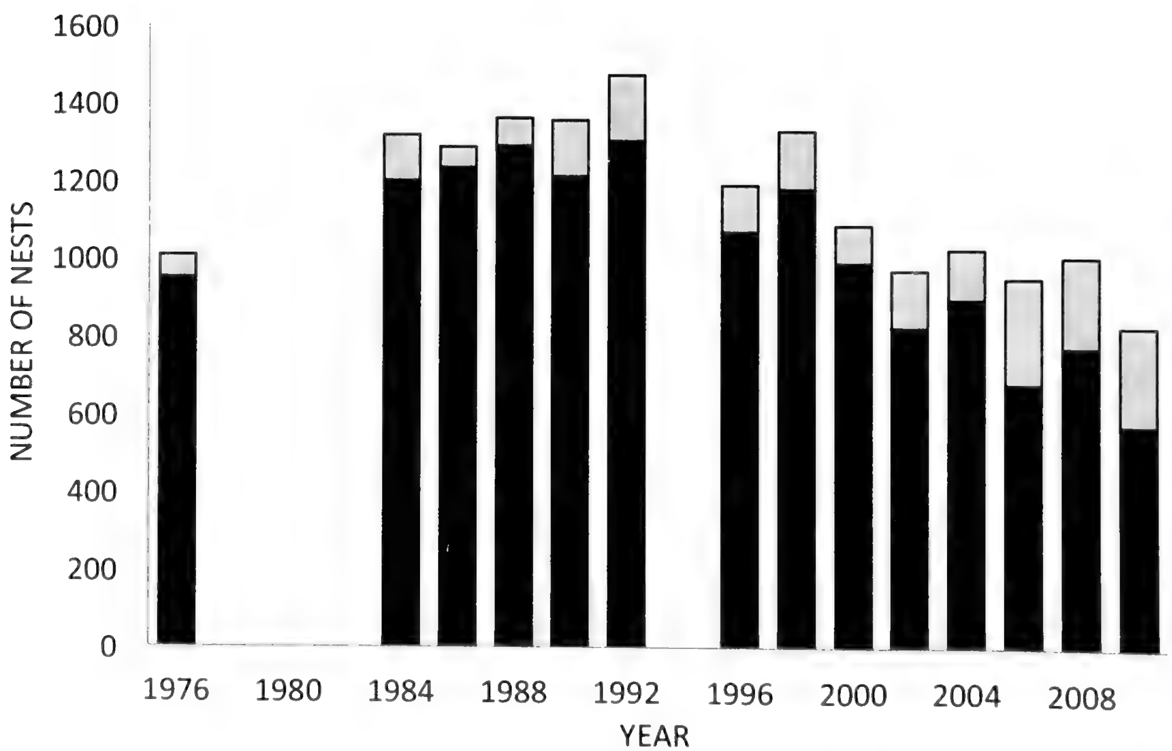

FIGURE 3. Comparison of occupied nests (solid bars) with empty nests (open bars) of Great Black-backed Gulls (*Larus marinus*) at Boot Island National Wildlife Area, 1976 to 2010.

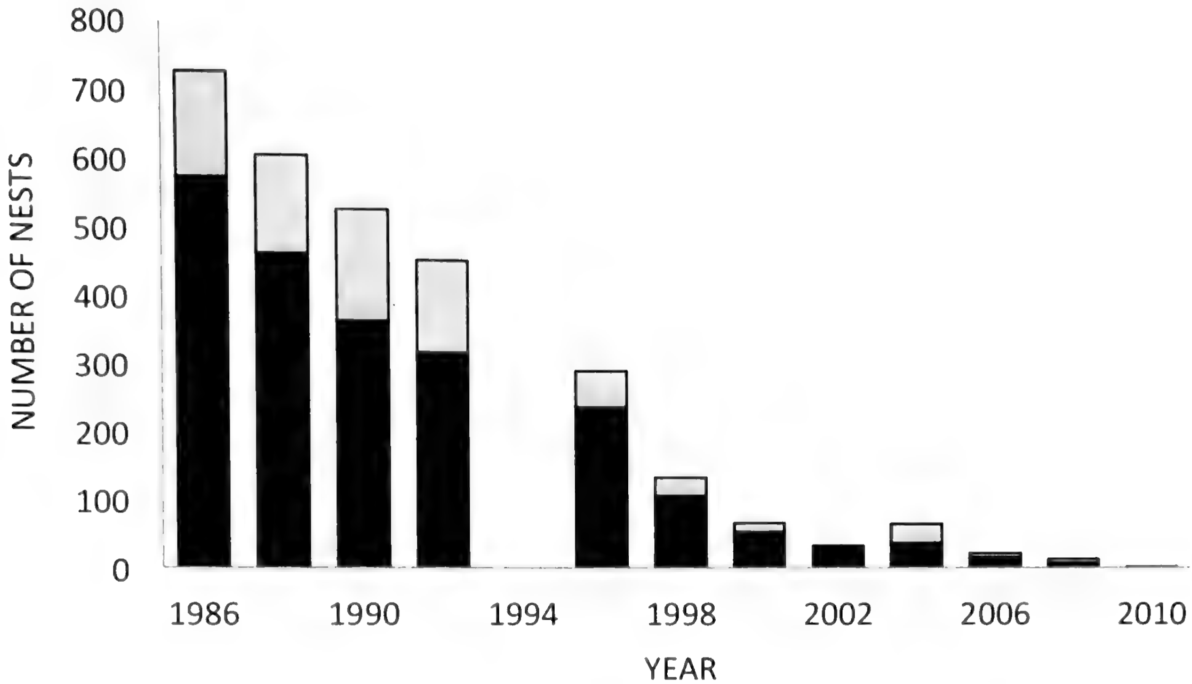

Figure 4. Comparison of occupied nests (solid bars) and empty nests (open bars) of Herring Gulls (*Larus argentatus*) at Boot Island National Wildlife Area, Nova Scotia, 1986 to 2010.

of the colony played a significant role in the observed reductions in gull numbers.

The cod fishery

In 1992 the North Atlantic Cod (*Gadus morhua*) population collapsed and the Canadian government placed a moratorium on the fishery. Chapdelaine and Rail (1997) were able to link this decline in the Atlantic cod fishery on the north shore of the Gulf of St. Lawrence with similar changes in nesting Herring Gull numbers on nearby islands. We do not know where the Boot Island Herring Gulls spend their time outside the breeding season, although some birds may winter along the eastern seaboard of the United States (see Drury and Nisbet 1973*; Gaston *et al.* 2008*). It may, however, not be coincidental that the rapid decline in Herring Gull numbers on the north shore of the Gulf of St. Lawrence from 1988 to 1993 (Chapdelaine and Rail 1997; Cotter and Rail 2007) roughly coincides with the Boot Island population crash from 1987 to 2002. Furthermore, changes observed at the Boot Island colony generally reflect regional trends for Great Black-backed and Herring Gulls in Nova Scotia from 1971 to 2002 (Cotter *et al.* 2012*).

Predation and disturbance

Coyote

The decline in both gull species coincide with the expansion of Coyote into Nova Scotia (Parker 1995). The range expansion and population increase of Coyotes in the province was rapid: provincial fur harvesters removed 777 animals in 1990–1991, with an increase to 1,887 animals in 1994–1995 (O'Brien and Boudreau 1998*). Coyotes are opportunistic predators (Berg and Chesness 1978; Parker 1995) and, in recent years, tracks and scat have been found on a number of offshore islands. Coyote sign (scat) was first recorded on Boot Island in 1998 with additional evidence (tracks and scat containing small bones) in 2000 and 2002. In 2004, one animal was observed feeding on Great Black-backed Gull eggs (MacKinnon *et al.* 2007). This animal readily swam across the narrow channel dividing Boot Island from the mainland and, on arrival, promptly started consuming gull eggs. The presence of Coyotes on the island during nesting is now likely a yearly occurrence, as one animal was observed in the gull colony in 2010 and again on 12 May 2014 (MacKinnon *et al.* 2010*).

American Mink and Raccoon

We also recorded the presence of American Mink on the island in 2004, 2008 and 2010 and, more recently, Raccoon in 2010. Both are notorious consumers of eggs and the young of ground-nesting birds and Raccoons have a significant impact on gull colonies (Kadlec 1971; Ellis *et al.* 2007). American Mink have also been predators in off-shore Nova Scotia tern colonies, such as those on Country Island and The Brothers (D'Eon 2005*).

Bald Eagle

Bald Eagles are frequently observed over Boot Island and, in 2008, a breeding pair took up residence in a large White Spruce (*Picea glauca*) adjacent to the gull colony. Eagles are known predators of gulls (Buehler 2000) and, although we did not observe a preda-

tion attempt during our surveys or search for prey remains under the nest, there was a conspicuous absence of gull nests in the immediate vicinity of the eagle nest. As approximately 50% of the gull colony is within 300 m of the eagle nest, the close proximity of eagles may influence the reproductive success of breeding gulls through disturbance of normal activities during the breeding season (White *et al.* 2006).

Egg collection by humans

Hébert (1989) reported that, among other factors, human predation on gull eggs for food (egging) was partly responsible for the observed decline in Herring Gulls on Kent Island, New Brunswick. No comparable activity has been reported for Boot Island, and we attribute this absence to the hazardous waters surrounding the island and the lack of an "egging tradition" in the largely agriculture-based adjacent community. Thus, egging is not considered to be a factor in the Boot Island gull decline.

Conclusion

Populations of nesting Great Black-backed and Herring Gulls have been in decline on Boot Island, Nova Scotia, for about 25 yrs. The earlier decrease in Herring Gull numbers may be attributed to aggression by the larger and competing Great Black-backed Gulls; however, declines in both species suggest that other, likely multiple, factors were involved. The loss of the Atlantic cod fishery in 1992 has been linked to gull declines in a number of colonies (Chapdelaine and Rail 1997) and this regional reduction of food availability may also be a contributing factor in the loss of Herring Gulls on Boot Island.

Coyote access to near-shore islands, following their expansion into Nova Scotia in the early 1980s, has resulted in nest loss from predation on Boot Island. Additional predation of eggs and chicks by American Mink, Raccoons, and Bald Eagles may have further contributed to an increase in nest failure in recent years. These stressors have become cumulative to the point that the Herring Gull colony on Boot Island has been essentially extirpated. In 2010, the Herring Gulls and nests were almost completely absent, while the Great Black-backed Gull colony had declined to 56% of its peak in 1990. It is important to note that this study is based on short duration field observations conducted over a number of years and that any definitive cause and effect is beyond the scope of this paper. Further work, such as determining the foraging and wintering areas of the Boot Island gulls is required.

A combination of many factors appears to be responsible for the observed declines. A broad reduction in food resources caused by changes in fisheries and better landfill management; the arrival of the Coyote along with other nest predators, such as American Mink and Raccoon; and the recent establishment of an active Bald Eagle nest within the colony may all have contributed to the observed decline in gulls on Boot Island.

Acknowledgements

The survey data for Boot Island National Wildlife Area have been collected with the assistance of a number of participants over many years. We thank the following crew leaders, staff, and volunteers for their efforts: Jeff Atkinson, Peter Barkhouse, Bill Barrow, Barb Boiduk, Susan Bowes, Adam Campbell, Cyril Coldwell, Donald Colpitts, Graham Daborn, Tony Erskine, Keith Galbraith, Jocelyne Gauvin, Gay Hanson, L. Hanson, Peter Hicklin, Randy Hicks, Matthew Horsman, Ron Hounsell, Etta Hudgins, Jason Hudson, Larry MacDonnell, Andrew Macfarlane, Nancy (Lutz) MacKinnon, Adam MacPherson, Randy Milton, Reg Newell, Darren Ogden, Cindy Pauley, Mark Pulsifer, Mathew Robinson, Sylvie Roussel, Vishalla Singh, Peter C. Smith, and Jim Wolford. Our apologies to those we may have missed. We also thank Paul Chamberland, Kevin Davidson, Tony Gaston, Peter Hicklin, and two anonymous reviewers for commenting on earlier drafts of this paper.

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Received 6 December 2013
Accepted 5 February 2014

Distribution and Abundance of Baling Twine in the Landscape Near Osprey (*Pandion haliaetus*) Nests: Implications for Nestling Entanglement

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Seacor, Renee, Kayhan Ostovar, and Marco Restani. 2014. Distribution and abundance of baling twine in the landscape near Osprey (*Pandion haliaetus*) nests: implications for nestling entanglement. Canadian Field-Naturalist 128(2): 173–178.

Polypropylene baling twine used by Ospreys (*Pandion haliaetus*) during nest construction creates a risk of entanglement for nestlings and adults on the Yellowstone River, Montana. In 2013, we evaluated the abundance of twine in 2-km-radius buffer zones centred on 38 nests for three categories of road density. We found more twine per kilometre along roads in low (n = 19) and moderate (n = 13) road density nest buffer zones than in high road density nest buffer zones (n = 6). The estimated total amount of twine found along roads in nest buffer zones ranged from 0 to 2602 m and did not differ among road density strata. The percentage of Osprey nests containing twine was highest in low (63.2%) and moderate (61.5%) road density nest buffer zones and lowest (33.3%) in high road density buffer zones, which reflected a gradient from rural and suburban to urban landscapes. The estimated total amount of twine within a nest buffer zone did not predict whether a nest contained twine. The amount of twine found in seven nests destroyed by wind or power company personnel ranged from 0 to 206 m and was not correlated with the amount of twine found in their buffer zones. During the 2012 and 2013 breeding seasons, four of 120 nestlings (3.3%) became entangled in twine: two were cut free and fledged normally, one died, and one was euthanized. The abundance of twine in the environment surrounding nests and its slow rate of biodegradation mean that vigilance by citizen scientist nest monitors and assistance from power companies are the only short-term solution to reducing mortality resulting from entanglement.

Key Words: baling twine; entanglement; Montana; mortality; Osprey; *Pandion haliaetus*; Yellowstone River

Introduction

Many bird species incorporate atypical materials into their nests (Hansell 2000). A variety of species use anthropogenic nesting materials, such as plastic trash, twine, and rope, and the prevalence of plastics in nests is thought to be increasing (Montevecchi 1991; Antczak *et al.* 2010; Votier *et al.* 2011). Because plastics degrade slowly, using the percentage of nests containing plastics as an index of their abundance in the environment over time requires both a constant search effort and knowledge of bird population trends (Ryan *et al.* 2009). Moreover, the presence of plastics in large, long-lasting nests suggests that such an index is best considered over decades rather than years (Bond *et al.* 2012). Although some individuals within a species benefit by signaling conspecifics through the use of artificial nesting materials (Hansell 2000), plastic rope and twine present a potential risk of nestling and adult entanglement. In fact, mortality associated with the use of these nesting materials is well documented in White Storks (*Ciconia ciconia*; Kwieciński *et al.* 2006), Northern Gannets (*Morus bassanus*; Votier *et al.* 2011), and Great Grey Shrikes (*Lanius excubitor*; Antczak *et al.* 2010).

The stick nests of Ospreys (*Pandion haliaetus*) often include both natural items (e.g., wings, bones, dung, and sod) and artificial objects (e.g., clothing, shoes, toys, and rope) (Allen 1892). The propensity of nesting Ospreys for using discarded polypropylene baling twine, which is used by farmers and ranchers to store hay and straw, has recently elicited some conservation concern. For example, all nests near agricultural fields at two study areas in Montana contained twine, which had entangled young in nearly 5% of nests (Blem *et al.* 2002). In west-central Saskatchewan, approximately 12% of nestlings had become entangled (Houston and Scott 2006). Both groups of researchers concluded that entangled nestlings would have died without human intervention. Baling twine hanging from Osprey nests on power poles has come into contact with electrical lines and is thought to have ignited fires, which further endangered nestlings (personal communication with power company linemen).

During visits to Osprey nests in 2012, we noticed that adults had often incorporated baling twine into nests. Various lengths of twine were found in the nest bowl, wrapped around large sticks, or hanging from the nest rim. Three out of 50 (6%) nestlings had become so badly entangled in twine that they had to be rescued, had died, or had to be euthanized (Figure 1). While driving between nests, we often observed remnants of baling twine along the shoulders of secondary roads. The prevalence of plastic string, rope, and twine in the environment surrounding nests has been cited as a reason for their occurrence in nests (Blem *et al.* 2002; Antczak *et al.* 2010; Bond *et al.* 2012), and our observations prompted us to investigate the abundance of discarded baling twine in the landscape surrounding Osprey nests. Our objectives were to estimate and com-

FIGURE 1. An Osprey (*Pandion haliaetus*) nestling badly entangled in baling twine and later euthanized, Yellowstone River, Montana, 2012. Compare the normal right foot and tarsus with the grossly swollen and disfigured left foot and tarsus. Photo: Cameron Sapp.

pare the amount of twine along roads near Osprey nests across a gradient from rural to urban landscapes and to assess the relation between the presence of twine in nests and the amount of twine found along roads near nests. Our results have allowed us and our partner, the Yellowstone Valley Audubon Society (YVAS), to target specific areas for cleanup and specific landowners for conservation education.

Study Area

The study area extended approximately 945 km along the Yellowstone River floodplain from the Wyoming–Montana border (44°59'29"N, 110°30'58"W) to the Montana–North Dakota border (47°45'28"N, 104°02'42"W). As the river flows downstream, it changes from a high-gradient, clear, cold mountain system to a low-gradient, turbid, warm-water system. The geomorphology of this dynamic, unregulated river comprises wide multi-channel reaches, forested islands, gravel bars, and straight channels with cliffs. Vegetation along the riparian corridor reflects the decrease in elevation, from higher-elevation (1750 m) forests dominated by conifers (e.g., *Juniperus*, *Pinus*, *Picea*, and *Pseudotsuga* spp.) to river bottoms (615 m) composed of a mixture of shrubs (e.g., *Salix* spp.) and deciduous trees (e.g., *Populus* spp.). Anthropogenic land uses along the river include small grain farming, livestock grazing, recreation, and urban-centred industries, such as oil refining and coal-fired power generation. Billings (population 106 000) is the largest city along the river and is situated near the middle of the study area. Climate is semi-arid.

Methods

Along with 15–20 citizen scientists from YVAS, we conducted fieldwork during the 2012 and 2013 breeding seasons. Beginning in April, we used binoculars and spotting scopes to survey the study area for nesting Ospreys. We used a Global Positioning System (GPS; Garmin GPSMAP 62) to record the location of nests and uploaded these coordinates into a geographic information system (GIS). Nests were observed from the ground at approximately 1-week intervals throughout the breeding season to determine occupancy (Steenhof 1987) and to estimate dates of egg laying, hatching, and fledging; brood size; and reproductive success, i.e., number of young fledged (Harmata *et al.* 2007).

We used ArcGIS (v. 10.1, Environmental Systems Research Institute, Redlands, California, USA) to create a 2-km-radius buffer zone around each of the 71 Osprey nests located in 2012 to identify roads for twine sampling. The size of the buffer zones was large enough to contain an adequate number and length of roads to survey based on our sampling protocol (see below) and small enough to allow us to survey the entire Osprey study population in one season. We obtained a state roads GIS from the Montana Geographic Information Clearinghouse (National Resource Information System 2013*), which categorized roads into seven types: United States Forest Service, primary, secondary, National Highway Administration non-interstate, interstate, city–county, and urban. The roads layer was added to the georeferenced nest buffer zones, and roads were then highlighted and clipped to each buffer zone. Because of safety considerations, we did not survey Interstates 90 or 94 and, therefore, for each buffer zone containing those roads, we subtracted their lengths from the total length of roads. We also omitted six nest buffer zones from further consideration because they contained less than 10 km of roads, the lower limit of our sampling protocol (see below). We partitioned the remaining 65 nest buffer zones into three road density

strata based on the total length of roads they contained: low, 10 to < 20 km; moderate, 20 to < 40 km; and high, ≥ 40 km). These categories spanned a gradient from agricultural land (rural) to cities (urban) across the heterogeneous study area.

We did not have any *a priori* information (e.g., variation in metres of twine per buffer zone) to guide sampling effort or allocate kilometres of road per stratum to survey for baling twine, which are required for Neyman-like optimization (Cochran 1977). Therefore, we used square-root of stratum size (i.e., total kilometres of road within each stratum) as a reasonable compromise between equal and proportional allocation of sampling effort (Bankier 1988). The allocated kilometres of road to survey for twine in each nest buffer zone (i.e., sampling effort) increased with road density stratum: low (10–12 km), moderate (14–16 km), and high (≥ 18 km). When the buffer zones of different nests overlapped by ≥ 20%, we randomly selected one zone to sample for baling twine, and then, in the field, we did not survey any road segments in the overlapping area to maintain statistical independence in analyses.

In the field during the 2013 nesting season, we used an iPad (Apple, A1430) and the ArcMap application to select and number sequentially each 2-km road segment within a nest buffer zone. A coin flip determined whether a particular segment was surveyed for baling twine, a process repeated up to the allocated number of kilometres to be surveyed for each buffer zone depending on its road density (i.e., low: 10 or 12 km, moderate: 14 or 16 km, and high: ≥ 18 km). For example, we surveyed either five or six 2-km road segments in each nest buffer zone in the low road density stratum for a total search effort of either 10 or 12 km. In a few instances, we were unable to survey a selected 2-km road segment because access was restricted. Alternative roads were randomly chosen where possible, but when these were unavailable, we reduced the number of kilometres surveyed in that zone. Travelling by bicycle allowed us to look for twine along both sides of selected roads. We collected twine from the road and pavement edge to fencing along the shoulder (about 4 m in width). Twine was bagged and labelled by nest buffer zone, and its length (to the nearest metre) was estimated with a tape measure in the laboratory.

Data transformations were unsuccessful in achieving normal distributions; thus, we used the Kruskal-Wallis independent samples test to determine whether the number of metres of baling twine collected per kilometre of road differed among the three road density strata (SPSS v. 19.0, IBM, Armonk, New York, USA). We conducted the same test to determine whether the total amount of twine in a buffer zone (i.e., metres of twine collected per kilometer of road multiplied by total kilometres of roads within a buffer zone) differed among road density strata. We used Dunn's test to identify differences in rank among the three road density strata following a significant Kruskal-Wallis test. Although Kruskal-Wallis is a ranks (not a means or median) test, we have provided box plots of data distribution to aid interpretation.

In 2013, we noted which Osprey nests contained baling twine during the banding of nestlings or by observation from the ground. We used logistic regression to examine the relationship between estimated total amount of twine in a buffer zone and the presence or absence of twine in the nest. Goodness of fit was evaluated using the Hosmer–Lemeshow test. We also measured the amount of twine (metres) in nests that had either blown down during storms or had been removed by power company personnel. We used linear and non-linear regression models to test for a relationship between the amount of twine in those nests and the amount of twine found along roads in the corresponding buffer zone (per kilometer of road and total). The significance of all statistical tests was accepted at $P < 0.05$.

Results

Together with YVAS volunteers, we surveyed approximately 925 km of the Yellowstone River for Osprey nests in 2012 and 2013. All nests considered in the baling twine analyses (n = 65) were built on artificial structures (i.e., power poles, nest platforms, or bridge spans). Of the buffer zones around these nests, 25 were located in areas of low road density (10 to < 20 km), 23 in areas of moderate road density (20 to < 40 km), and 17 in areas of high road density (≥ 40 km). The number of nests available for statistical analysis decreased after we omitted buffer zones that overlapped by ≥ 20%, leaving us with 19, 13, and 6 nests in the low, moderate, and high road density strata, respectively. The mean number of kilometres of roads surveyed for twine in each nest buffer zone varied across road density strata: low, 10.9 km (SD 0.7, range 10–12); moderate, 13.5 km (SD 1.2, range 14–16); and high, 21.3 km (SD 2.9, range 18–28).

The ranks (amount) of baling twine collected per kilometre of road surveyed within nest buffer zones differed among low, moderate, and high road density strata (H = 6.10, df = 2, P = 0.047); low road density buffer zones had significantly higher ranks than high road density buffer zones (Figure 2A). However, the ranks of estimated total length of twine in buffer zones did not vary with road density (H = 3.12, df = 2, P = 0.210) (Figure 2B). The percentage of Osprey nests containing twine was nearly twice as high in the low (63.2%, 12 of 19) and moderate (61.5%, 8 of 13) road density strata as in the high road density stratum (33.3%, 2 of 6).

The total amount of baling twine estimated within a nest buffer zone did not predict whether a nest contained twine (χ^2 = 0.36, df = 1, P = 0.547). Although the data fit the logistic regression model, only 23 of 38 nests (60.5%) were classified correctly; all but one contained twine. We observed 93.7% more nests without

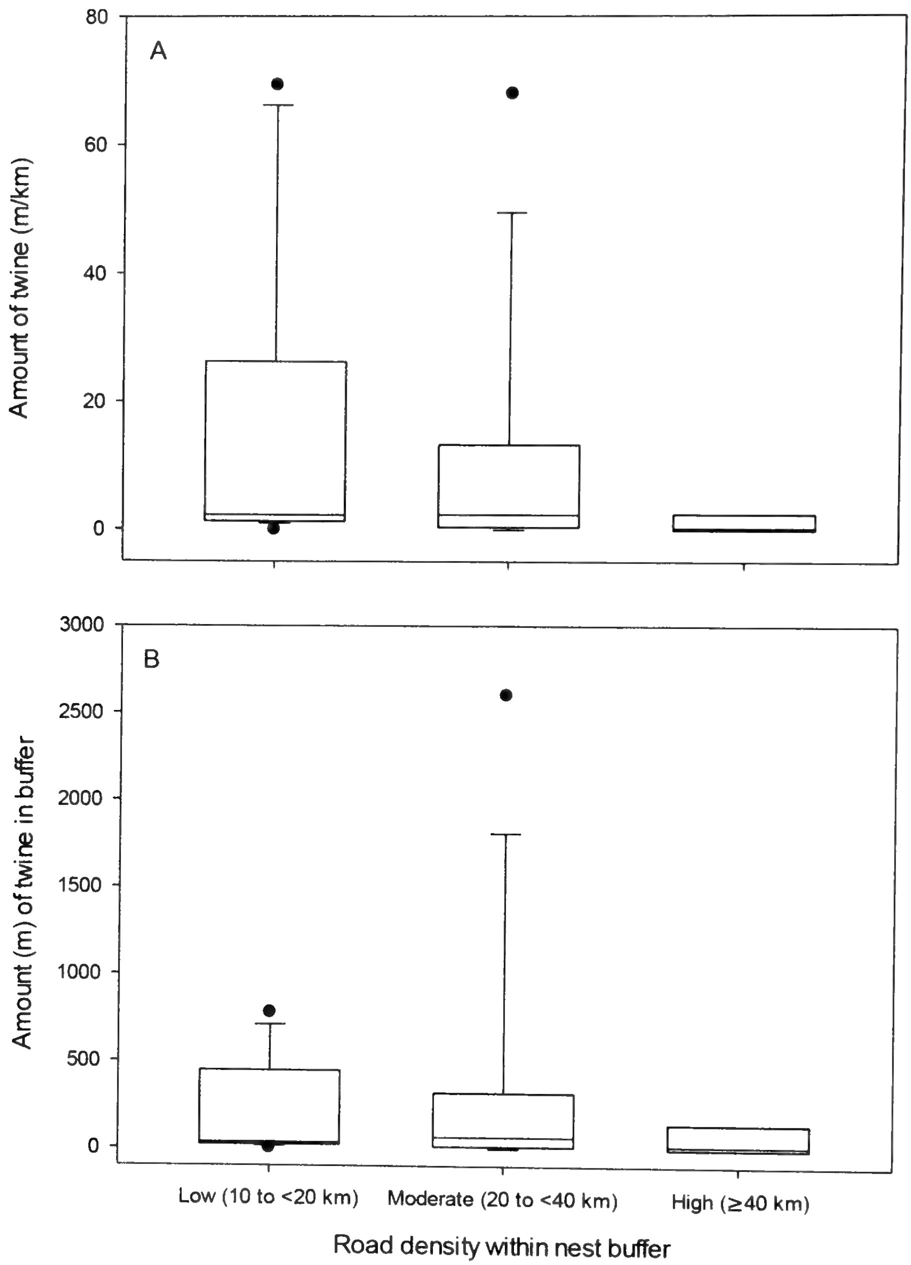

FIGURE 2. Amount of baling twine in 2-km-radius buffer zones around Osprey (*Pandion haliaetus*) nests along the Yellowstone River, Montana, 2013. A: Metres of twine per kilometre of road; B: Estimated amount of twine (m) in buffer zones. Note: lines indicate median, boxes show the 25th and 75th percentiles, whiskers indicate the 10th and 90th percentiles, and dots show outliers.

twine (15 of 16 nests) than predicted by the model. We collected twine from seven nests that had either blown down in storms or were removed by power company personnel before or after the nesting season in 2013 (Table 1). No relationship existed between the amount of twine found in nests and either the amount of twine found per kilometre of road (linear: $F = 1.01$, df = 1, $P = 0.362$; non-linear: $F = 1.03$, df = 1, $P = 0.357$) or the total amount estimated in nest buffer zones (linear: $F = 1.05$, df = 1, $P = 0.353$; non-linear: $F = 1.09$, df = 1, $P = 0.354$).

Ospreys occupied 28 nests in 2012 and 50 nests in 2013; the large increase in the number of occupied nests located in 2013 reflects the greater field effort on the part of the citizen scientists. Ospreys fledged an average of 1.8 nestlings per occupied nest in 2012 and 1.4 nestlings per occupied nest in 2013. During 2012, two of 21 (9.5%) successful nests contained three nestlings entangled in twine: one was found dead during the banding visit, one had to be euthanized, and one was cut free and appeared to fledge normally (three of 50 [6.0%] nestlings entangled). During 2013, one

TABLE 1. Amount of baling twine found in Osprey (*Pandion haliaetus*) nests blown down during storms or removed by power company personnel and the estimated amount of twine in a 2-km-radius buffer zone around each nest, Yellowstone River, Montana, 2013.

	Length of twine, m		
Nest ID no.	In nest	Per km of road in buffer zone	In buffer zone
137	0	0.2	5
295	1	3.4	63
318	1	1.8	22
350	206	2.2	43
354	0	2.3	52
374	131	26.3	447
598	64	4.3	74

of 35 (2.9%) successful nests contained an entangled nestling; it was cut free and appeared to fledge normally (one of 70 [1.4%] entangled nestlings).

Discussion

We found significantly more baling twine per kilometre of road in Osprey nest buffer zones in low and moderate road density areas than in high road density areas, which reflected the gradient from rural and suburban to urban landscapes. Although we did not find a direct relationship between the estimated total amount of twine in a buffer zone and its presence in nests, the percentage of nests containing twine was highest in rural and suburban areas and lowest in urban areas. The amount of twine found along roads surrounding nests varied considerably: rural buffer zones, 0–778 m; suburban buffer zones, 0–2602 m; and urban buffer zones, 0–506 m.

From our observations in 2012, we knew that baling twine accumulated along roads, and this prompted us to initiate this study, the first to estimate twine abundance near Osprey nests. Surveying roads was convenient and efficient. We believe that measuring the amount of twine found along roads near nests underestimated its abundance in the landscape, because adjacent pastures and feedlots often contained discarded twine. An untested assumption of our study was that a positive relationship exists between the amount of twine along roads and the amount of twine in the 2-km-radius buffer zones around nests.

Most farmers and ranchers on our study area store hay and straw in large, round bales, each of which is a potential source of twine for nest-building Ospreys. A single bale contains approximately 115 m of twine (Houston and Scott 2006). One hay bale can feed one horse or steer per month during winter; therefore, five horses fed for five months require approximately 25 bales (and 2875 m of twine). It remains unclear how twine is transferred from pastures and feedlots to roads, but we suspect that most had blown off the flat beds of ranch pickup trucks, where we often observed it loosely coiled or piled. In fact, we observed one such instance while conducting twine surveys. Regardless of the mechanism, Ospreys in southern Montana encounter an abundant and apparently available resource for use as nesting material.

Without human intervention, 3.3% of Osprey nestlings on the Yellowstone River would have died from twine entanglement, which is lower than the 11.7% nestling mortality reported by Houston and Scott (2006) in Saskatchewan. In our study, the percentage of successful nests in which young were entangled (5.4%) was higher than that reported from nearby central Montana (4.6%; Blem et al. 2002). Current estimates of mortality resulting from entanglement on the Yellowstone River does not appear to be of conservation concern regarding the potential for additive mortality because the Osprey population had reproductive rates in 2012 and 2013 greater than those needed to support a stable population (Henny and Wight 1969; Postupalsky 1989). However, twine entanglements did raise animal welfare concerns because nestlings and adults suffered slow deaths from starvation, constriction, and infection. The only practical, short-term solution strategy to prevent deaths from entanglements is to have citizen citizen-scientist volunteers regularly visit nests and contact us if they observed entangled nestlings. In each such instance, power company cooperators have responded quickly to our requests for assistance.

The amount of baling twine we collected from seven nests that had been destroyed by wind or removed by power company personnel varied by two orders of magnitude (0–206 m per nest). Similar variation was reported in the mass of plastics found in five nests constructed by Northern Gannets (Votier *et al.* 2011). Several proximate factors have contributed to the extent that artificial materials are used in nest construction or as nest adornments: abundance in the environment (Blem *et al.* 2002; Bond *et al.* 2012), age of the nest (Votier *et al.* 2011; Bond *et al.* 2012), and age of the nest builder (Sergio *et al.* 2011). On the Yellowstone River, no relationship existed between the amount of twine found in the landscape and the amount found in Osprey nests. We lacked information on the age of nests, but it appeared that larger nests, which were presumably older, contained more twine; however, the limited sample of seven nests made this inference tentative. Although we found a variety of anthropogenic materials in nests, the largest component was baling twine, and such selectivity has been noted in a diversity of bird species from seabirds to raptors to passerines (e.g., Antczak *et al.* 2010; Sergio *et al.* 2011; Votier *et al.* 2011; Bond *et al.* 2012). Whereas the cost of using baling twine in Osprey nests was clear, any potential benefits have yet to be determined (e.g., conspecific signaling; Sergio *et al.* 2011).

Educating the public about the risks that baling twine presents to nesting Ospreys is a component of our research project. Together with our partner, YVAS, we mail informational brochures to landowners along the

Yellowstone River, with the hope of promoting responsible handling and disposal of twine. We are also identifying what we believe are significant sources of the twine that ends up along roads (e.g., feedlots). Polypropylene baling twine degrades slowly and clean-up efforts along roads and in pastures and feedlots will have to be coordinated for decades to reduce dangers to Ospreys (see also Ryan *et al.* 2009; Bond *et al.* 2012). It appears that farmers and ranchers are slowly switching from using twine to bale hay and straw to using plastic netting or wraps. We rarely find the latter materials in nests and view such a transition as a potential long-term solution benefitting Ospreys.

Acknowledgements

This project was a cooperative effort between the Yellowstone River Research Center (Rocky Mountain College) and the Yellowstone Valley Audubon Society. We thank C. Sapp and the dozens of citizen scientists who dedicated countless hours in the field to monitoring nests in 2012 and 2013. W. Newton, statistician at the Northern Prairie Wildlife Research Center (United States Geological Survey), kindly volunteered his time and expertise to design the twine sampling protocol. He, A. Harmata (Montana State University) and two anonymous reviewers provided valuable comments on the draft manuscript. Generous in-kind support was provided by Beartooth Electric Cooperative, Montana–Dakota Utilities, NorthWestern Energy, Park Electric Cooperative, Yellowstone Valley Electric Cooperative, and Yellowstone Valley Tree Surgeons. Many landowners, the United States Bureau of Land Management, the city of Billings, and the Audubon Education and Conservation Center graciously granted permission to monitor and access nests on their properties. This research was approved by the Institutional Animal Care and Use Committee at Montana Fish, Wildlife and Parks (IACUC FWP07-2012) and through a Montana Scientific Collector's Permit (2013-031) to K. Ostovar and a Federal Bird Banding Permit (22513) to M. Restani. Funding was provided by the Yellowstone River Research Center, Toyota TogetherGreen, The Cinnabar Foundation, The Peregrine Fund, Yellowstone Valley Audubon Society, Montana Audubon, Rocky Mountain College, St. Cloud State University, and Montana Fish, Wildlife and Parks.

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Received 7 December 2013
Accepted 31 January 2014

Cues used by Predators to Detect Freshwater Turtle Nests may Persist Late into Incubation

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Riley, Julia L., and Jacqueline D. Litzgus. 2014. Cues used by predators to detect freshwater turtle nests may persist late into incubation. Canadian Field-Naturalist 128(2): 179–188.

Previous studies have found that turtle nest depredation is concentrated immediately post-oviposition, likely because cues alerting predators to nest presence are most obvious during this time. In Algonquin Provincial Park, Ontario, we examined the frequency of nest depredation during the incubation period for Snapping Turtles (*Chelydra serpentina* [Linnaeus, 1758]) and Midland Painted Turtles (*Chrysemys picta marginata* [Agassiz, 1857]). Contrary to most past findings, nest depredation occurred throughout the incubation period for both species. In fact, 83% and 86% of depredation interactions with Snapping and Painted Turtle nests, respectively, occurred more than a week after oviposition at our study site. Peaks in nest depredation (weeks with ≥10% nest depredation) occurred late in incubation and may have coincided with hatching. Trail cameras deployed at four nesting sites revealed six predator species interacting with nests. The presence of predators at nest sites increased late in the incubation period indicating a persistence or renewal (from hatching) of cues; additional research is necessary to determine the nature of these cues. These findings have implications for both research and turtle conservation. Further research should examine the relationship between temporal changes in predator species' density and patterns of nest depredation. Additionally, in areas where protective nest caging is used as a species recovery action, it may be important to ensure that cages remain in place throughout the incubation period until emergence of hatchlings.

Key Words: Snapping Turtles; *Chelydra serpentina*; Midland Painted Turtles; *Chrysemys picta marginata*; Turtles; Algonquin Provincial Park; Ontario; ecology; nest depredation; predator detection; predators; species recovery

Introduction

Freshwater and marine turtles are among the most at-risk groups of vertebrate animals, and one of the many threats to turtle populations is unnaturally high levels of nest predation (Gibbons *et al.* 2000; Spotila 2011). A broad range of animals from multiple taxa depredate turtle nests, including mammals, birds, reptiles, and invertebrates (Ernst and Lovich 2009). High levels of turtle nest depredation commonly occur in human-disturbed landscapes because food resources associated with human presence (e.g., trash, agricultural crops) increase the abundance of subsidized predators of turtle eggs (Christiansen and Gallaway 1984; Garber and Burger 1995; Mitchell and Klemens 2000; Seburn 2007; Fordham *et al.* 2008; Kurz *et al.* 2011). In addition, the removal of top predators in urban areas has caused an increase in the number of mesopredators, leading to a concomitant increase in depredation of turtle eggs (Barton 2003; Prugh *et al.* 2009; Ritchie and Johnson 2009). In some turtle populations, subsidized mesopredators annually depredate 100% of nests (e.g., Geller 2012), resulting in chronic prevention of recruitment (Spinks *et al.* 2003; Seburn 2007; Fordham *et al.* 2008). Substantial repeated reductions in recruitment (approximately a 50% or more decrease in egg and/or hatchling survival) perpetuate population declines (Crouse *et al.* 1987; Crowder *et al.* 1994; Tomillo *et al.* 2008). World-wide and in Canada, turtle populations are in decline (Gibbons *et al.* 2000); thus, it is important to understand all possible threats, including the ecology and behaviour of nest predators, to increase the effectiveness of management and recovery actions.

Many studies of turtle nest depredation report that most depredation events occur within the first week post-oviposition (Tinkle *et al.* 1981; Christens and Bider 1987; Congdon *et al.* 1983, 1987; Robinson and Bider 1988; Burke *et al.* 2005; Strickland *et al.* 2010; Geller 2012; Wirsing *et al.* 2012; Holcomb and Carr 2013). For example, Congdon *et al.* (1983) found that 87% of Blanding's Turtle (*Emydoidea blandingii*) nest depredation occurred within the first 5 days post-oviposition. Congdon *et al.* (1987) found that of depredated Snapping Turtle (*Chelydra serpentina*) nests, 59% were depredated within the first 24 h, 73% of these nests were depredated within the first 6 days, and 100% by the 32nd day post-oviposition. Robinson and Bider (1988) found that 57% of depredation events occurred within 72 h of nest construction, and 87% occurred within 5 days post-oviposition. Similarly, Desroches and Picard (2007) found that 80% of nests were depredated in the first week post-oviposition. Holcomb and Carr (2013) found that 86% of Alligator Snapping Turtle (*Macrochelys temminckii*) nests were depredated within the first 24 h, and, on average, the time until depredation was 19 h.

The high peak of depredation immediately post-oviposition is thought to occur because cues alerting predators to the presence of a nest are most prominent at this time. These cues might include olfactory stimuli, such as the scent of oviposition fluid (Legler 1954; Congdon *et al.* 1983; Spencer 2002), and visual cues, such as the presence of a female turtle (Congdon *et al.* 1987; Eckrich and Owens 1995) and soil disturbance

(Strickland *et al.* 2010; Spencer 2002). Acceptance of this evidence has led some researchers examining cues for nest depredation (e.g., Marchand and Livaitis 2004; Strickland *et al.* 2010) to base their methodology on the premise that depredation of turtle nests is restricted to the first week post-oviposition. For only 2 weeks, Marchand and Livaitis (2004) monitored fake nests constructed to investigate depredation, and Strickland *et al.* (2010) monitored nests for 2 days post-oviposition. Yet, is an early peak the only temporal pattern of turtle nest depredation reported in the literature?

Although most studies of nest depredation report that it occurs within a short time post-oviposition, a few, largely neglected, studies document substantial levels of nest depredation throughout or late in the incubation period. Snow (1982) found that 55% of depredated Painted Turtle (*Chrysemys picta*) nests were older than 3 days; however, all of the nests were still depredated within the first month of incubation. Brooks *et al.* (1992) found that all Wood Turtle (*Glyptemys insculpta*) nest depredation occurred 9 weeks after the last nest was laid. Burger (1977) found that the risk of depredation of Diamond-backed Terrapin (*Malaclemys terrapin*) nests did not decrease over the course of incubation; instead, nest depredation was significantly higher 60–90 days post-oviposition (75% of remaining nests depredated) than 1–30 days and 30–60 days post-oviposition (27% and 20% of nests within those periods, respectively). Gillingwater (2002) observed nest predation throughout the incubation period and, in some cases, Northern Map Turtle (*Graptemys geographica*) nests were depredated the following spring after hatchlings had overwintered in the nest. Some reports document bimodal predator activity, with peaks around nesting and hatching. For example, Congdon *et al.* (1983) found that a few nests (6%) were depredated at the end of the incubation period during hatchling emergence and, similarly, Desroches and Picard (2007) found that 5% of freshwater turtle nests were depredated during hatchling emergence. In these studies, because of a large peak in nest depredation immediately post-oviposition, there may not have been many nests left to depredate in the fall. Also, nest debris may make nest-searching by predators more challenging.

Nevertheless, predators often appear to cue in on nests later in incubation. During fieldwork for a 41-year study of the ecology of Snapping Turtles and a 35-year study of Midland Painted Turtles (*Chrysemys picta marginata*) based out of the Wildlife Research Station (WRS, 45°35'N, 78°30'W) in Algonquin Provincial Park, Ontario (R. J. Brooks, University of Guelph and J. D. Litzgus, Laurentian University), field technicians observed that nest depredation was occurring throughout incubation. These observations and our subsequent review of the literature led to our research question: do predators detect nest cues that persist long after oviposition and lead to later occurrences of nest depredation?

In the long-term Algonquin Park study, eggs are removed from the nest cavity less than 4 h post-oviposition, measured, and reburied within 24 h (Samson *et al.* 2007). This study method is common in turtle research, management, and conservation programs globally; thus, depredation patterns documented in our study may be representative of what is occurring under these circumstances. This method also provides the unique opportunity to examine the temporal pattern of nest depredation that occurs when fresh cues left by the mother are reduced. The aim of our project was two-fold: first, to quantify the frequency of nest depredation throughout incubation for Snapping and Midland Painted Turtles when nest cues are reduced immediately post-oviposition and, second, to compare this temporal pattern to patterns reported previously to determine if nest cues and depredation peaks are present later in incubation.

Study Area

The study took place along the Highway 60 corridor on the west side of Algonquin Provincial Park, Ontario, Canada. The study area is within the Algonquin–Lake Nipissing ecoregion, which is a rugged landscape underlain by Precambrian Shield outcrops (Ontario Ministry of Natural Resources 1998). Forest cover dominates, with predominantly upland mixed forests of sugar maple (*Acer saccharum*), yellow birch (*Betula alleghaniensis*), and eastern hemlock (*Tsuga canadensis*) and lowland sites with spruce (*Picea* spp.) and tamarack (*Larix laricina*) (Hughes 2003). Field sampling was concentrated at two sites: the WRS and Arowhon. The WRS is within the North Madawaska watershed and nesting sites in this area vary from natural sand dunes beside lakes to gravel embankments along access roads and Highway 60. At the Arowhon site, nesting occurs on a decommissioned rail-line that is used as a public hiking trail (Mizzy Lake Trail; Schwarzkopf and Brooks 1985). Elevations on the west side of Algonquin Park (370 – 570 m above sea level) are higher than the surrounding landscape and experience a cool and wet climate (Ontario Ministry of Natural Resources 1998); this climate is reflective of the northern range limits of both turtle species.

Methods

From 30 May to 4 July 2011, Snapping and Midland Painted Turtle nesting was monitored daily. Nest sites were monitored visually by researchers on foot and using binoculars. Monitoring occurred from dawn (about 0500) to about 1000, and from just before to dusk (about 1700) until after dark, as long as nesting activity was occurring, to capture the time frames in which Snapping and Painted Turtles experience peak nesting (Ernst and Lovich 2009). The nesting activity of each female was recorded as it occurred. Nest locations were marked with metal stakes and flagging tape. Nests were carefully excavated, maintaining the eggs

in the same order and orientation in which they were found (Samson *et al.* 2007). After the eggs were removed, the nest cavities were filled with soil excavated during egg removal. The eggs were taken to a field laboratory to record clutch data for the long-term study (egg data were not used in the current study). Eggs were reburied in their original nest chambers within 24 h post-oviposition, before the vitelline membrane adhered to the inner shell surface and formed a "white spot" on the top of the egg (Yntema 1964; Rafferty and Reina 2012), thus ensuring no trauma to developing embryos (Samson *et al.* 2007). We cannot discount the possibility that removal, processing, and reburial of eggs by researchers in the first 24 h affected depredation rates, especially at the start of incubation. Although we present data for the first 72 h post-oviposition, we are aware they may not be indicative of depredation rates on nests from which eggs were not removed (Congdon *et al.* 1983; Tinkle *et al.* 1981; Christens and Bider 1987; Burke *et al.* 2005; Strickland *et al.* 2010; Geller 2012; Wirsing *et al.* 2012).

Each nest was randomly assigned to a caging treatment (above ground, below ground, or wooden-sided cage, or uncaged control) and cages were deployed when the eggs were reburied (69 Midland Painted Turtle and 52 Snapping Turtle nests). Various nest cage types were used to test their effects on hatchling fitness for another study (Riley and Litzgus 2013); here we report only the details of predator interactions with these nests. During the nesting season (June) and the hatching season (September), the nests were monitored daily for predation attempts and successful depredation events. During the remainder of the incubation period (July and August), the nests were monitored weekly (Burke *et al.* 1998; Kolbe and Janzen 2002) because of logistic constraints. A depredation attempt was recorded when substrate was cleared away from around the nest or nest cage and/or the nest cage was dug up but the predator did not reach the nest chamber (Figure 1A). A successful depredation event was recorded when eggs were dug up and/or eaten (Figure 1B). If predator tracks and scat were discernible

FIGURE 1. A. An above-ground nest cage with substrate cleared away from the sides indicating a depredation attempt. B. Successful depredation of a nest protected by a wooden-sided cage indicated by the excavated nest chamber and eggshell fragments. C. A trail camera photograph of a Red Fox (*Vulpes vulpes*) interacting with a nest outfitted with an above-ground cage. All photographs were taken during summer 2011 in Algonquin Provincial Park, Ontario, Canada.

around a nest, the predator species was identified and recorded. To gauge the predator assemblage patrolling the nesting sites and to capture interactions between predators and nest cages, four trail cameras (119456C, Bushnell Corporation, Overland Park, Kansas, USA) were set-up from 1 July to 1 October 2011 at four nest sites.

The numbers of depredation attempts and successful depredation events were combined for analysis to create a total number of depredation interactions. This total did not differ among cage types or from the uncaged control nests over the incubation period (Riley and Litzgus 2013). It was assumed that if the nest cages were not protecting the clutches, a depredation attempt would have been successful. If a nest was subject to multiple depredation attempts (i.e., a predator targeted the same nest multiple times), only the first attempt was included in the dataset.

We quantified predator interactions with nests in two ways. First, we used a non-parametric product-limit survival analysis (Kaplan and Meir 1958; Engeman *et al.* 2006). The survival time equaled the time (days) from oviposition to the first predator interaction. When eggs hatched, those nests were considered "censored" after the time of that event, and thus removed from the analysis. A Mann–Whitney–Wilcoxon test was used to compare the survival curves between species. Second, we undertook a more detailed analysis of the specific timing of the depredation interactions during incubation. This part of the analysis included only nests that were subject to depredation interactions during incubation (Snapping Turtle, 29/52 nests; Midland Painted Turtle, 28/69 nests). For each species, the number of depredation interactions was totaled for each week of incubation (29 May to 1 October 2011). This number was divided by the total number of depredation interactions over the incubation period and multiplied by 100 to calculate the percentage (i.e., frequency) of depredation interactions that occurred weekly. For each species, this observed distribution of depredation frequency was compared with an expected distribution based on previous quantified reports of depredation in the literature, using a Kolmogorov–Smirnov goodness-of-fit test. From all literature sources that contained usable data, we averaged the reported data to generate an expected distribution of depredation interactions by week post-oviposition (Table 1). Also, using a Kolmogorov–Smirnov goodness-of-fit test and our data, we compared the distribution of weekly depredation interactions post-oviposition for Snapping Turtles with that for Midland Painted Turtles to determine whether there were differences in pattern. Depredation peaks were identified as weeks with $\geq$ 10% nest depredation. A significance level of $\alpha = 0.05$ was used for all statistical tests. Statistical analyses were performed using R (R Foundation for Statistical Computing, Vienna, Austria).

For predator interactions where tracks or scat were identified, the number of interactions observed for each predator species was summarized monthly. Similarly, the number of photographs of each predator species taken by the trail cameras was summarized monthly to elucidate temporal patterns of predator presence at the nest sites over the course of incubation.

Results

For both turtle species, the probability of nest survival decreased steadily with number of days post-oviposition (Figure 2). The survival curves did not differ between species ($W_1 = 365$, $P = 0.11$). In 2011, the first Snapping Turtle nest was found on 7 June, and the last nest was found on 24 June. The observed frequency of weekly predator interactions with Snapping Turtle nests over the incubation period was different than the expected distribution of depredation interactions post-oviposition ($D = 0.63$, $P < 0.01$; Figure 3A). For Midland Painted Turtles, the first nest was found on 2 June and the last was found on 2 July. The observed frequency of weekly predator interactions with Midland Painted Turtle nests over the incubation period

TABLE 1. Rates of turtle nest predation over the course of incubation reported in previously-published studies. The means of these rates were used to create an "expected distribution" of depredation frequencies for comparison with our observed frequencies for Snapping Turtles and Midland Painted Turtles in Algonquin Provincial Park using a Kolmogorov–Smirnov goodness-of-fit test. For the purposes of the test, the mean depredation frequency estimated for weeks 4+ (3.7%) was split over weeks 4–16 (0.3% each week).

Study	Species	Depredation frequency (%)			
		Week 1	Week 2	Week 3	Week 4+
Congdon *et al.* 1983	Blanding's Turtle	87	5	4	4
Christens and Bider 1987	Painted Turtle	86	0	0	14
Burke *et al.* 2005	Diamond-backed Terrapin	100	0	0	0
Wirsing *et al.* 2012	Snapping Turtle	98	1	0	1
	Painted Turtle	98	1	0	1
Geller 2012	Map Turtle spp.	90	7	0	3
Snow 1982	Painted Turtle	64	21	12	3
Mean expected distribution used in Kolmogorov–Smirnov test		89	5	2.3	3.7

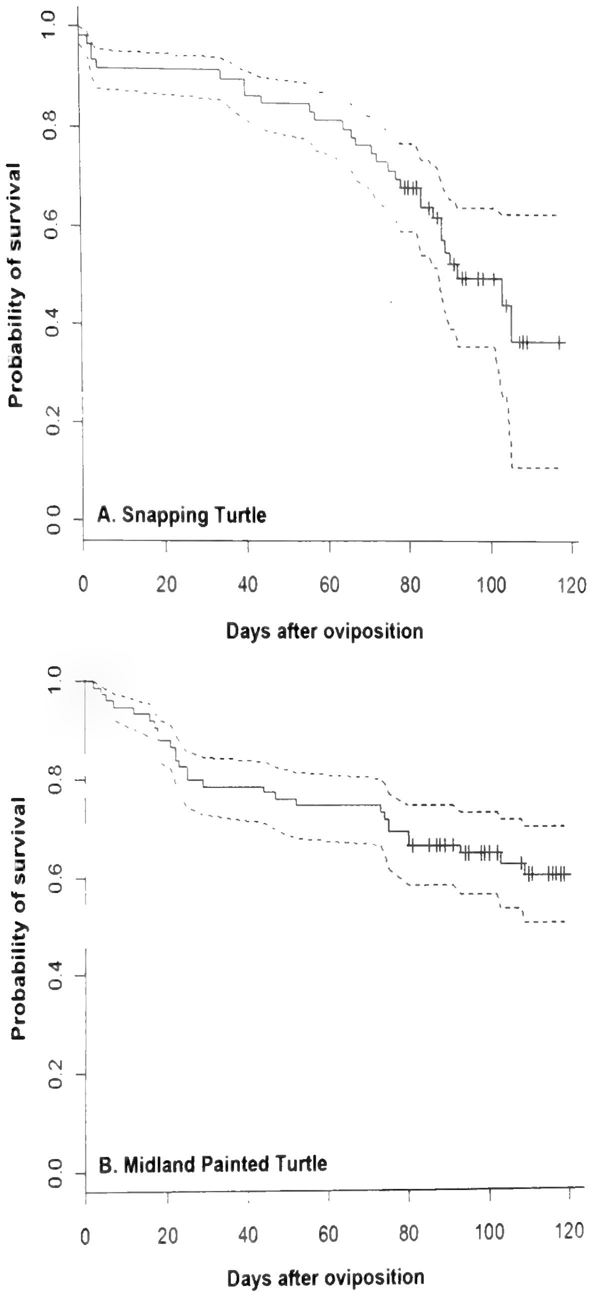

FIGURE 2. Survival curves (solid lines) for (A) Snapping Turtle (*Chelydra serpentina*) and (B) Midland Painted Turtle (*Chrysemys picta marginata*) nests over the incubation period in Algonquin Provincial Park. Vertical tick marks indicate when eggs hatched and their nest was "censored" from the analysis. The grey area represents the period when hatchlings were emerging from the nests. Dashed lines indicate standard errors.

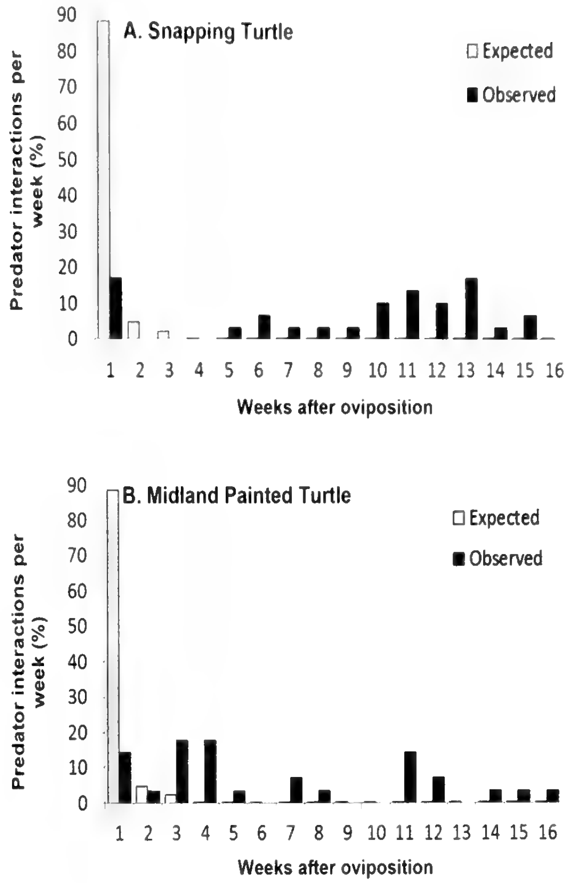

FIGURE 3. For (A) Snapping Turtle (*Chelydra serpentina*) and (B) Midland Painted Turtle (*Chrysemys picta marginata*) nests in Algonquin Provincial Park, observed weekly frequencies of predator interactions over the incubation period (29 May to 17 September 2011) were significantly different from those expected based on previous reports (see Table 1 for list of studies). The grey area represents the period when hatchlings were emerging from the nests.

was also different from the expected distribution ($D = 0.63$, $P < 0.01$; Figure 3B).

For Snapping Turtle nests, 17% of predator interactions occurred in the first week post-oviposition. Another peak of predator interactions (weekly interactions ranging from 10% to 17% of the total depredation interactions) occurred from weeks 10 to 14 (64 to 91 days) post-oviposition. Predator interactions occurred throughout the incubation period up to 105 days post-oviposition. For Midland Painted Turtle nests, 14% of predator interactions occurred in the first week post-oviposition. Another spike in predator interactions occurred 3 and 4 weeks post-oviposition, when 18% of total depredation interactions occurred each week. Another peak in depredation occurred at 11 weeks (71 77 days) post-oviposition, when 14% of total depredation interactions occurred. We also observed elevated levels of predation in week 12 (7% of total depredation interactions). Similar to Snapping Turtle nests, predator interactions with Midland Painted Turtle nests occurred throughout incubation until 109 days post-oviposition. The number of predator interactions per week over the incubation period did not differ between species ($D = 0.31$, $P = 0.42$).

Six predator species were identified interacting with nests and were present at the study sites throughout

incubation: Red Fox (*Vulpes vulpes*), Eastern Wolf (*Canis lycaon*), Raccoon (*Procyon lotor*), American Crow (*Corvus brachyrhynchos*), Common Raven (*Corvus corax*), and Wild Turkey (*Meleagris gallopavo*) (Figure 4). The number of photographs of predators at nest sites captured by the trail cameras was highest in August and September; specifically, the number of photographs of canid (Red Fox and Eastern Wolf) predators increased during this time. Of the predator interactions for which species were identified, Red Foxes were the most common predators of nests from July until the end of incubation.

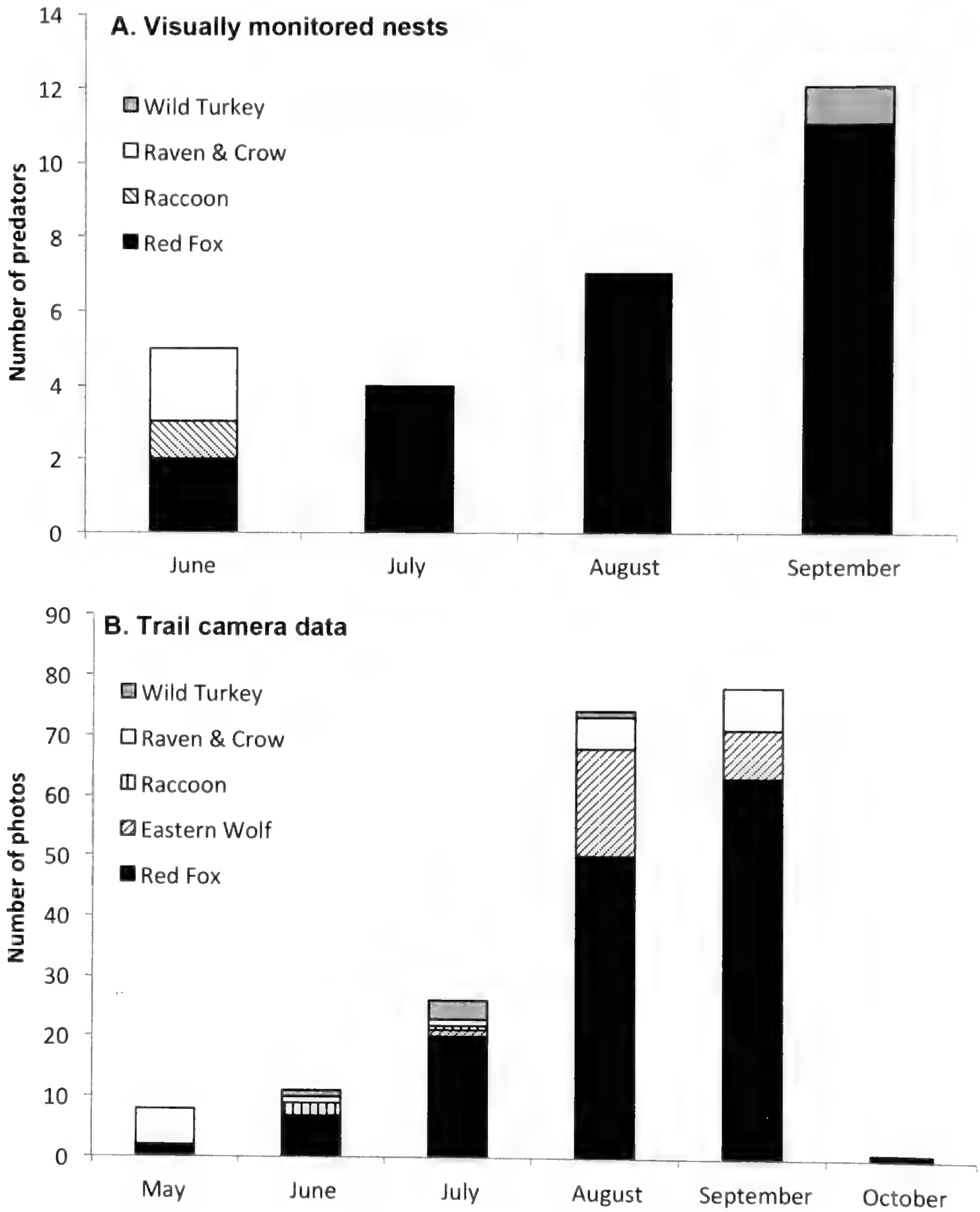

FIGURE 4. Assessment of the predator assemblage at Snapping Turtle (*Chelydra serpentina*) and Midland Painted Turtle (*Chrysemys picta marginata*) nesting sites in Algonquin Provincial Park by (A) number of predators identified from tracks and scat interacting with nests and (B) number of photographs taken by trail cameras of each predator species by month over the incubation period.

Discussion

We observed nest predation throughout incubation, and there were peaks in depredation (one for Snapping Turtles and two for Midland Painted Turtles) more than a week after oviposition. Our observed patterns of nest predation were atypical compared to those generally reported in the literature. Only a handful of other published studies have reported nest predation throughout or late in incubation (Snow 1982; Burger 1977). Also, the presence of predators at nest sites in our study, particularly canid species, increased later in incubation (August and September). These later peaks in depredation may be a result of a larger predator population at this time of year because canid pups begin to hunt independently in the fall (C. Callaghan pers. comm.), and because predators are somehow cueing to nests at hatching. Wild dogs have been documented to target Leatherback Sea Turtle (*Dermochelys coriacea*) and Green Sea Turtle (*Chelonia mydas*) nests during hatching and to dig up nests and prey on hatchlings before their emergence from the nest (Spotila 2011). Burger (1977) found that crows and gulls depredated terrapin nests only during oviposition, whereas mammals (raccoons and foxes) depredated nests at a low rate during oviposition and at a high rate during hatching. Also, mammalian predators depredated Wood Turtle (*Glyptemys insculpta*) nests 9 weeks post-oviposition (Brooks *et al.* 1992). In our study, removing eggs from nests in the first 24 h post-oviposition (which may have reduced early-incubation nest depredation) provided an opportunity to investigate depredation in the later stages of incubation.

It appears that cues to nests exist and can be detected by predators throughout egg incubation, but what are these cues? The most obvious answer may be that the predator-exclusion cages around several of the nests monitored in our study may have served as visual cues to the nests' presence. However, our study also included nests with no cages and nests protected by cages that did not extend above ground (Riley and Litzgus 2013) and, therefore, did not provide a visual cue. Indeed, predation interactions did not differ among the nest caging treatments, including controls with no cages (Riley and Litzgus 2013); thus, it does not appear that predators were using nest cages as visual cues to a food source. Other researchers have also found that marking nests did not increase depredation rates (Burke *et al.* 2005; Strickland *et al.* 2010). In contrast, raccoons, coyotes, and *Corvus* sp. have been found to use nest cages and nest markers, respectively, as visual cues for nests (Mroziak *et al.* 2000; Rollinson and Brooks 2007; S. D. Gillingwater, pers. comm.). This is most likely a learned response (Rollinson and Brooks 2007), and it appears that, at our study site, predators have not yet learned to associate nest cages, which were present for only 2 summers, with the presence of turtle eggs.

A few other studies that examined unprotected turtle nests also found that nest predation occurred late in incubation (Snow 1982; Burger 1977; Brooks *et al.* 1992); thus, a natural cue must be attracting predators to nests at that time. For Midland Painted Turtles, the depredation peak at 3–4 weeks post-oviposition could be associated with predators returning to the nesting sites when these turtles lay their second clutches (approximately 2 weeks after the first clutch is deposited at our study sites; Brooks *et al.*, unpublished data). The return of nesting female turtles may present a visual cue for predators. The presence of hatchlings at a nesting site may also act as a visual cue for predators later on in incubation and trigger further searching and predation of nests. At Rondeau Provincial Park and Long Point, Ontario, raccoons and coyotes have been observed following the tracks of early-emerging turtles back to their natal nest and consuming the remaining eggs and young (S. D. Gillingwater, pers. comm.).

How else would predators know where unmarked turtle nests are located? Embryonic fluids released during hatching could serve as olfactory cues to attract predators to nests in August and September. In addition, rotting undeveloped or unfertilized eggs may produce olfactory cues. At our study sites, canid presence increased in August and September, and this group of animals is well-known for its outstanding olfactory abilities (Spotila 2011). Another possibility for nest detection may be auditory cues. Some turtle hatchlings have recently been reported to vocalize within the nest cavity after hatching (Ferrara *et al.* 2013).

In our study, the later peak in predator interactions with nests was found at 64–94 and 71–77 days post-oviposition for Snapping and Painted Turtles, respectively. These peaks of depredation precede the beginning of hatchling emergence for Snapping Turtles (77 days post-emergence; Riley *et al.* unpublished data) by 13 days, and for Midland Painted Turtles (74 days post-emergence; Riley *et al.* unpublished data) by 3 days. Thus, these peaks could correspond to the release of embryonic fluids (olfactory cues) and potential vocalization by hatchlings (auditory cues). The study by Brooks *et al.* (1992) lends support to this idea, as mammalian predators began depredating nests at their study site 9 weeks after the last nest was completed, which corresponds to the hatching period and hatchling emergence for Wood Turtles (Ernst and Lovich 2009). Although this is a convincing association, it is impossible to correlate definitively the later peak in predator interactions with the hatching period from our study alone, as it is unknown when the eggs were hatching. Hatchlings often remain in the nest chamber after hatching, sometimes emerging 1–9 days later (Burger 1976; Christens 1990) or, in the case of Painted Turtles, in the spring after overwintering in the nest (Storey *et al.* 1988; Costanzo and Lee 1995; Costanzo *et al.* 2000; Packard and Packard 2003, 2004). Future work should examine olfactory, auditory, and visual cues at nests throughout incubation to determine whether the presence or types of cues change with time.

In our study, given that we potentially changed the nest cues during the first 24 h post-oviposition, we were able to measure peaks in nest depredation later in incubation for two freshwater turtle species. For Snapping Turtles, there was a later peak in nest depredation 10–14 weeks post-oviposition, and, for Midland Painted Turtles, there were peaks in nest depredation during weeks 3, 4, and 11 post-oviposition. There was also an increase in the number of canid predators at the study sites during these later peaks in incubation, which corroborates the findings of other studies in which mammal predator presence at nest sites increased before hatchling emergence from nests (Spotila 2011; Burger 1977). We report that there were comparatively low peaks in nest predation during the first week post-oviposition: only 17% and 14% of depredation interactions with Snapping and Midland Painted Turtle nests, respectively, occurred at this time. Some researchers have observed similar trends at other study sites, with nest predation occurring both during nesting and hatchling emergence (Burger 1977; Spotila 2011; Congdon *et al.* 1983; Desroches and Picard 2007). At various sites, differences in predator species densities and interspecific differences in the cues used by predators to find nests (i.e., avian species using visual cues, and mammal species using visual and olfactory cues) may be responsible for geographic variation in depredation frequency over incubation. Depredation frequency may also depend on individual predator behaviours and how they vary among sites. More research is needed to examine the effects of predator species and predator behaviour on temporal patterns of nest predation.

Management of at-risk turtles throughout North America commonly includes the use of cages to protect nests from subsidized mesopredators (Seburn 2007; Riley and Litzgus 2013). Some strategies suggest removal of nest cages halfway through incubation, as it is thought that depredation will not occur during the last half of incubation. In a study by Rahman and Burke (2010), nest protectors were removed from nests after 21–25 days of incubation, and, in one study area (out of three), depredation significantly increased in the 11 nights after nest protector removal. Engeman *et al.* (2006) also found that after removing nest cages from sea turtle nests, depredation rates increased substantially. Soil disturbance during nest cage removal may provide a cue to attract predators (Rahman and Burke 2010). An alternative to removing nest cages partway through incubation is including an opportunity for turtles to escape from the cage (e.g., escape hatches or holes). Our study, as well as others that document nest depredation before hatchling emergence, indicates that turtle nests can be at risk of depredation throughout the full incubation period. Thus, it is important to understand and study depredation timing at each location, as it may be site or predator specific, to gauge the effectiveness of a particular nest protection method for that site. In some areas, species recovery may require that nest protection measures remain in place throughout incubation and extend to hatchling emergence.

Acknowledgements

All work was carried out in compliance with the Canadian Council for Animal Care guidelines and under approved Laurentian University Animal Care Committee protocol 2008-12-02. All work was authorized by permits from the Ontario Ministry of Natural Resources (OMNR). Financial support for this work was provided by the Natural Sciences and Engineering Research Council, the Canadian Wildlife Federation, the OMNR's Species at Risk Stewardship Fund, the Toronto Zoo, and Laurentian University. In-kind contributions were provided by the Wildlife Research Station (WRS) in Algonquin Provincial Park and the University of Guelph. We thank R. J. Brooks for allowing access to his long-term study sites. Thanks also to the following people who assisted with fieldwork: K. Hall, M. Keevil, H. McCurdy-Adams, P. Moldowan, L. Monck-Whipp and staff and volunteers from the WRS. Thanks to J. Baxter-Gilbert, C. Davy, P. Moldowan, S. Gillingwater, and an anonymous reviewer for their helpful comments on the manuscript.

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Received 11 January 2014
Accepted 25 January 2014

Notes

A Gray Wolf (*Canis lupus*) Delivers Live Prey to a Pup

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Mech, L. David. 2014. A Gray Wolf (*Canis lupus*) delivers live prey to a pup. Canadian Field-Naturalist 128(2): 189–190.

A two-year-old sibling Gray Wolf (*Canis lupus*) carefully captured an Arctic Hare (*Lepus arcticus*) leveret alive on Ellesmere Island, Nunavut, Canada, and delivered it alive to a pup 28–33 days old. This appears to be the first observation of a Gray Wolf delivering live prey to a pup.

Key Words: *Canis lupus*; Gray Wolf; Arctic Hare; *Lepus arcticus*; learning; feeding; Ellesmere Island; Nunavut

The capacity to hunt and kill is innate in canids, as anyone who has raised a domestic dog (*Canis lupus familiaris*) can attest (Fox 1969). However, because of the difficulty of observing young free-ranging carnivores hunting and killing, information about the role of learning in helping fine-tune these behaviors is still developing (Caro and Hauser 1992; Thorton and Raihani 2008), and I know of no such information on Gray Wolves (*Canis lupus*).

Several felid species bring live prey to kittens (Kitchener 1999). Meerkats (*Suricata suricatta*) feed disabled scorpions (of the genera *Parabuthus* and *Opistophthalamus*) to pups (Thornton and McAuliffe 2006). Bat-eared Foxes (*Otocyon megalotis*) bring live invertebrates to their young (Nel 1999; Pauw 2000), and Red Foxes (*Vulpes vulpes*) allow cubs to capture live earthworms (MacDonald 1980). The phenomenon is discussed and the literature is summarized in Caro and Hauser (1992) and Thornton and Raihani (2008).

In Gray Wolves, the canine teeth are usually fully emerged by about 7 months of age (Van Ballenberghe and Mech 1975), and we know that by winter, when young-of-the year are 7–10 months old, they accompany adults and participate in the hunting and killing of prey (MacNulty *et al.* 2009). Even without parents present, 8- or 9-month-old Gray Wolves can kill White-tailed Deer (*Odocoileus virginianus*) (M. Jimenez, personal communication).

Young Gray Wolves accompanying adults probably learn to perfect their killing technique by observing the adults during the actual attacking and killing, and probably by imitating them. Yearling Gray Wolves seen up close while helping their parents kill a Muskox (*Ovibos moschatus*) calf bit the calf as close as possible to where their parents were biting it on the head (Mech 1988, page 78), even though no Gray Wolf was biting any other part of the body and the head holds were not lethal.

Although the basic killing tendency is innate in carnivores, gaining experience at an early age would be adaptive because prey is often so difficult to find, catch, and kill that any advantage at any step in the process would promote survival. Thus the following observation of a two-year-old sibling Gray Wolf providing a pup 28–33 days old (the pup's ears had only begun to stand upright 1–2 days before) with an opportunity to handle a live Arctic Hare (*Lepus arcticus*) is informative. I made the observation on 6 July 1994 on Ellesmere Island, Northwest Territories (now part of Nunavut), Canada, where I studied human-habituated Gray Wolves around dens close-up each summer from 1986 through 2010 (Mech 1988, 1995, 2005).

The primary prey of those Gray Wolves was Muskoxen and Arctic Hares, and the composition of the pack attending the den under observation during the present study was a breeding male and female (named Whitey), a two-year-old female (Explorer), a two-year-old male, and a single pup (Mech 1995). It was common for the adults to catch and quickly kill young Arctic Hares, and I had watched Explorer do so several times both as a yearling and as a two-year-old (Mech *et al.*, in press).

Following are my observations as edited from my field notes:

6 July 1994, 1534—I left the north side of the den ridge and started toward a hill to the east. Explorer followed me and, when 150–250 m from the den, surprised an Arctic Hare leveret about 20 cm long which jumped up and fled. Explorer chased it for 4 minutes back and forth along a creek bed and valley, catching it several times with her paws, grasping it with her mouth, shaking it, and dropping it. She could have killed it several times but did not. Each time that she dropped the hare it ran again, and she had to re-catch it. Finally she secured it alive.

Just as Explorer caught the leveret, Whitey came running down from the den (around 300 m away) and chased Explorer trying to snatch the Arctic Hare. Whitey was unable to catch Explorer, and Explorer took the Arctic Hare to the den. My assistant observing from another vantage point saw Explorer carry the live leveret by the nape of the neck toward the den. She dropped it on the way and re-caught it, and then delivered it alive to the pup. The pup was very interested in the leveret and tried to eat it. Explorer eventually grabbed the leveret from the pup, and she and the pup chewed it. At some point during this process the leveret died.

The obvious question about this observation is why Explorer spent so much time and effort keeping the leveret alive. Explorer found the leveret close to the den, and the leveret was small. Both circumstances were favorable for the live delivery. Delivering a small live prey animal to a pup would serve to introduce the pup to live prey when the prey is helpless, and that would allow the pup to learn that the active animal represents food. An alternative explanation suggested by a reviewer is that "the juvenile rabbit triggered several incomplete responses, with behavioral elements of (a) prey killing, (b) food delivery, and (c) pup carrying." It was not clear whether the pup or Explorer actually killed the leveret, but the killing took place some time soon after the pup encountered the animal alive. Simple learning would have allowed the pup to associate pawing the live leveret with feeding.

To my knowledge this is the first observation of a Gray Wolf delivering live prey to a pup. Such behaviors might not be common in Gray Wolves, because this incident is the only time I have seen it during 13 summers observing Gray Wolves and dens in the area for 2–6 weeks each year. On the other hand, even though I have seen Gray Wolves kill Arctic Hares about 25 times, I have never seen a Gray Wolf capture a leveret so close to a den before.

This observation fits the definition of opportunistic teaching (Caro and Hausner 1992), in that the two-year-old Gray Wolf modified her behavior in the presence of a pup with no killing experience without an immediate benefit to herself and provided the pup with experience, thus helping the pup improve its basic predatory skill.

Acknowledgements

This study was funded by the U.S. Department of the Interior. I also thank Environment Canada and the Polar Continental Shelf Project for logistical support; Craig Johnson for his assistance with observations; and Dan Stahler and two anonymous reviewers for offering helpful suggestions to improve the manuscript.

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Received 8 August 2013
Accepted 8 November 2013

Assessing Capture Success of Small Mammals Due to Trap Orientation in Field–Forest Edge Habitat

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Wolcott, Daniel M., Madison R. Ackerman, and Michael L. Kennedy. 2014. Assessing capture success of small mammals due to trap orientation in field–forest edge habitat. Canadian Field-Naturalist 128(2): 191–194.

The prediction that trap orientation would not affect the likelihood of capturing small-nonvolant mammals in field–forest edge habitat was tested during late May and early June 2010 at 3 locations in western Tennessee. Traps were placed in pairs along transects in edge habitats with the orientation of one trap facing outward, toward the field, and the other oriented inward, toward the forest. Results reflected no differential capture success due to trap orientation among ages, sexes, species, or locations. This finding should facilitate the inventorying and monitoring of small mammals in an abundant and potentially species-rich habitat type found in many terrestrial regions.

Key Words: capture success; edge habitat; Sherman live trap; small mammal monitoring; trap success; trap susceptibility; trap orientation

Introduction

Adjoining field and forest habitats (field–forest edge) are common throughout many ecoregions. Generally, variety and abundance of life are thought to be greatest in and about edges (Smith and Smith 2012). However, the intensity, or even presence, of edge effects has been questioned by many recent studies (reviewed in Murcia 1995). Although field–forest edges are sites with the potential for high biodiversity, the increase in such sites due to habitat fragmentation raises the risk of deleterious effects on resident communities (Groom *et al.* 2006).

Field–forest edges are interesting sites for studying aspects of biodiversity and sustainability of small mammal populations. Murcia (1995) and Fagan *et al.* (1999) noted the need for investigations in edge habitats. Many studies of natural history traits require live capture and examination of individual animals. Choosing an effective, unbiased trapping method is important for collecting reliable information on populations of small mammals (Risch and Brady (1996). Wilson *et al.* (1996) described procedures for measuring and monitoring biological diversity; however, they did not discuss orientation of live traps in detail. At this time, the significance of trap orientation to capture success in field-forest edge habitats is unknown.

The transition zone between field and forest habitats often contains thick vegetation, which may be easier to access from the field side. When sampling for small mammals with live traps in many field–forest edges, investigators must decide whether to place the traps with opening toward the field or the forest. Given that visibility and accessibility are greater from the field side, traps are usually approached from this direction to reduce the time and effort needed to check and rebait them. The extra effort required to access a trap opening that faces the forest is worthwhile if capture success is enhanced but not if it is decreased or insignificant. Therefore, the purpose of our investigation was to test the prediction that trap orientation (opening of the trap facing the field or the forest) has no effect on the likelihood of capturing small, non-volant mammals (hereafter, small mammals) in field–forest edge habitat.

Study Area

The study was conducted at three locations in western Tennessee: Ames Plantation, Meeman Biological Station, and Shelby Farms Park (hereafter, Ames, Meeman, and Shelby Farms, respectively). Ames was located in Fayette and Hardeman counties (35°6.9'N, 89°12.7'W); Meeman (35°21.7'N, 90°1.1'W) and Shelby Farms (35°8.4'N, 89°50.2'W) were in Shelby County. All locations represented sites with numerous anthropogenic field–forest edge habitats. At Ames, fields were either currently used for agriculture or were early successional habitat. Forests consisted mainly of mature bottomland hardwoods with some upland hardwood forests (Baldwin *et al.* 2005). At Meeman, fields consisted of maintained areas with some early successional habitat, and forests comprised mature upland and bottomland hardwood forests (Carver *et al.* 2011). Shelby Farms was the study area with the greatest anthropogenic influence. Fields there were created by current agricultural practices or were maintained areas or road edges, and forests comprised upland and bottomland hardwood forests (Wolcott *et al.* 2012). Habitats examined in our investigation represented a mosaic of field–forest edge types in both rural and urban locations.

Methods

Trapping

Our trapping protocol consisted of transect-sampling using Sherman live traps (7.5 cm × 9.0 cm × 23.0 cm; H. B. Sherman Traps, Inc., Tallahassee, Florida) following the method of Jones *et al.* (1996). During late May and early June 2010, traps were placed along 54 transects in pairs with one trap facing the forest and the other oriented toward the field. Each

transect included 30–40 total traps with pairs of traps spaced approximately 5 m apart. Trap placement was fully randomized throughout the study with an even number of transects having the field-facing trap on the left-hand side and other transects having the field-facing trap on the right side. All traps were placed with the door mechanism free from obstructions to ensure efficient operation. Traps were baited with rolled oats and checked daily.

We conducted sampling for 1–3 nights along each transect. Number of trap-nights (i.e., one trap set for one night) was used as a metric to maintain equal comparisons between the two trap orientations. Species, age, and sex of captured animals were determined. Animals were temporarily marked on the ventral surface (lightly) with a black or blue sharpie marker (Sanford LP, Oak Brook, Illinois) and released at the site of capture. We followed the guidelines for the use of wild mammals in research suggested by the American Society of Mammalogists (Sikes *et al.* 2011) and the Institutional Animal Care and Use Committee of the University of Memphis approved our methods (IACUC Protocol 0673).

Analysis

Logistic regression was used to assess capture success based on trap orientation. The dependent variable was categorized as binary: capture success of a field-facing trap was coded as 0, and capture success of a forest-facing trap was coded as 1. The predictor variables for sex, age, location, and species were coded as dummy variables (see Sokal and Rohlf 2012). Ages were categorized as juvenile, sub-adult, or adult (see Martin *et al.* 2002). Reference categories were adult for age, female for sex, Ames for location, and House Mouse (*Mus musculus*) for species. Logistic regressions considered possible demographic factors (sex, age, and species) as well as locale, which could account for differences in capture success due to trap orientation. The goodness-of-fit for each logistic regression was assessed using a likelihood ratio test (Sokal and Rohlf 2012). All statistical tests were performed in R version 3.0.2 (R Foundation for Statistical Computing, Vienna, Austria, 2012).

Results

Sampling effort (orientation of traps equally divided) was 10216 trap-nights: Ames 1596, Meeman 2280, Shelby Farms 6340. In total, 408 individual small mammals (191 males, 217 females) were captured a total of 480 times (230 males, 250 females): captures at each location were Ames 147 (65 males, 82 females); Meeman 75 (38 males, 37 females); Shelby Farms 258 (127 males, 131 females). A total of six species were captured. The White-footed Mouse (*Peromyscus leucopus*) was captured most often (n = 324; 157 males, 167 females) followed by the Hispid Cotton Rat (*Sigmodon hispidus*; n = 80; 33 males, 47 females), the Woodland Vole (*Microtus pinetorum*; n = 40; 19 males, 21 females), the North American Deermouse (*Peromyscus maniculatus*; n = 23; 13 males, 10 females), the House Mouse (n = 9; 6 males, 3 females), and the Marsh Oryzomys (*Oryzomys palustris*; n = 4; 2 males, 2 females).

Likelihood ratio tests conducted for each model showed that neither demographic factors nor location significantly increased the likelihood of capture success in a particular orientation: sex L = 0.441, df = 1, P = 0.507; age L = 1.016, df = 1, P = 0.602; species L = 3.602, df = 1, P = 0.608; location L = 0.362, df = 1, P = 0.835).

Discussion

Our results support the prediction that trap orientation does not affect the capture success of small mammals in relation to age, sex, species, or location in field–forest edge habitat. Rana (1986) and Norton (1987) showed that small mammals do not use areas randomly and that well-placed traps will enhance capture success. Capture success for this group of mammals is also influenced by several factors other than placement (see Wilson *et al.* 1996). For example, sampling may vary among habitat (e.g., Feldhamer *et al.* 1993; Schnell *et al.* 2008). Capture rates are also known to be different for males and females (Davis and Emlen 1956). Males often have larger home ranges than females and, thus, greater exposure to traps. Because of this, males are often captured more frequently than females resulting in sex biases in trapped samples (Buskirk and Lindstedt 1989; Poindexter *et al.* 2013). Our findings suggest that a sex bias is not present in the successful capture of individuals at a particular orientation.

Differential capture among species may be related to population density, with the most abundant species generally being captured in greatest numbers (see Nichols 1986; Hopkins and Kennedy 2004). As in our investigation, LaMountain (2007) reported that the White-footed Mouse was abundant in edge and forest habitats and the Hispid Cotton Rat was abundant in field habitat in western Tennessee. Other studies have recorded high densities of White-footed Mouse in edge (e.g., Adler and Wilson 1987; Manson *et al.* 1999) and forest sites (e.g., Yahner 1992; Wolf and Batzli 2002). Foster and Gaines (1991) and Brady and Slade (2001) noted an abundance of Hispid Cotton Rat in field habitats. In our study, we were able to capture species that are abundant in each of these habitat types. Our findings demonstrate that there was no significant difference in captures between the two trap orientations due to species.

Other factors are known to influence the capture of small mammals. For example, trap type (Sealander and James 1958; Hansson and Hoffmeyer 1973), type of bait (Churchfield 1990), moonlight (Price *et al.* 1984), chemical odours (Chabreck *et al.* 1986, Heske 1987), fire (Christian 1977; Gates and Tanner 1988), and weather (Gentry *et al.* 1966; Doucet and Bider 1974). In addition, Barnett and Dutton (1995) noted the im-

portance of trap position, spacing, quantity, and duration in the capture of small mammals. Because orientation of the trap could be a consideration in several of these untested factors, additional investigations of trap orientation in relation to trapping methods could provide new insight into procedures for studying small mammals in various habitats.

Overall, we found no difference in capture success due to trap orientation in field–forest edges in relation to age, sex, species, or location. It appears that the orientation of a trap in field–forest edge habitat makes little difference in the capture of small mammals. Given this finding, we note that orienting trap openings toward the field will likely minimize the trapping effort associated with checking and rebaiting traps. This information should be useful in future studies relating to the challenging tasks of surveying and monitoring populations of small mammals.

Acknowledgements

We thank the personnel of the Ames Plantation, Meeman Biological Station, and Shelby Farms Park for permission to work on lands under their control. We also thank A. Christopher Grow, as well as students from the University of Memphis field techniques course, who assisted in various aspects of the fieldwork associated with our investigation.

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Received 7 November 2013
Accepted 3 January 2014

Effect of Food Patch Discovery on the Number of American Crows (*Corvus brachyrhynchos*) Using a Flight Lane

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Langley, William. 2014. Effect of food patch discovery on the number of American Crows (*Corvus brachyrhynchos*) using a flight lane. Canadian Field-Naturalist 128(2): 195–199.

In winter, American Crows (*Corvus brachyrhynchos*) move back and forth between night roosts and foraging sites along flight lanes. If communal roosts act as information centres, we would expect more birds to use a particular flight lane after discovery of a new food patch on that route. In this study, I investigated how the number of crows using different flight lanes was affected by the establishment of artificial food patches, as well as how crows responded to multiple days of provisioning and to the location of the food patch relative to the flight lane. After discovery of a food patch, the number of crows using the flight lane closest to it increased, while numbers using adjacent flight lanes remained the same or decreased, particularly when the patch was in the path of the flight lane and when food provisioning occurred for 2 consecutive days. These results support the idea that crows using winter roosts may make use of information on food availability obtained at the roost.

Key Words: American Crow; *Corvus brachyrhynchos*; flight lane; winter roost; food patch; communication

Introduction

During the winter, American Crows (*Corvus brachyrhynchos*) gather in night roosting groups consisting of thousands of birds (Kalmbach 1916; Haase 1963). They move to and from these night roosts in flight lanes: in the morning they radiate out to foraging areas and in the evening congregate at pre-roosting aggregation areas before flying to the night roost (Aldous 1944; Moore and Switzer 1998). In some cases, crows use the same flight lane regularly; in other cases, they change flight lanes (Aldous 1944; Stouffer and Caccamise 1991; Caccamise *et al.* 1997). Large increases in the number of crows using a flight lane have occurred, after a food patch such as grain spilled from a railcar or an un-harvested sunflower field, was discovered (Langley 1992*).

An important potential function of a communal roost is that it can act as an information centre to facilitate finding and exploiting new food sources (Ward and Zahavi 1973; Weatherhead 1983). Common Ravens (*C. corax*) and Hooded Crows (*C. corone*) that have discovered a food patch recruit others at the night roost to follow them to the food patch the next day (Marzluff *et al.* 1996; Sonerud *et al.* 2001). Crows can also learn by "local enhancement", i.e., by watching other individuals and responding if a food patch is discovered (Richner and Marclay 1991). The fact that tagged crows at a food patch do not stay together at the pre-aggregation site or roost raises the possibility that more fluid kinds of interactions may also occur among individuals at a large roost (Moore and Switzer 1998).

The information centre hypothesis predicts that, after discovery of a food patch on a flight lane, more birds would use that lane subsequently. In this study, I investigated how the number of crows using a flight lane is affected by the location of a provisioned food patch relative to the lane and the number of days over which it is provisioned. The approach was to present a food patch just after a snow storm when wheat plants (*Triticum aestivum*) and un-harvested sorghum seed (*Sorghum bicolor*), the two main food items for crows during winter (Platt 1956), became less available.

Study Area

The study area was located in the northeast quadrant of the area surrounding a winter roost at Wichita, Kansas, where as many as 25000 birds a night have roosted over the past 50 years (Langley 1999). The area forms a rectangle of 969 km^2 including northeastern Sedgwick County and the western edge of central Butler County (Figure 1). Land use consisted of agriculture (mainly wheat and sorghum fields), pasture, small farms, residences, and several small towns (Langley 1992*). Observations occurred from December to March, 1990–1998.

Methods

Food patches were set out before dawn on the morning after a snowfall of at least 8 cm. A food patch consisted of 65 kg of corn kernels or bakery items. Food was spread over cleared frozen ground or on crusted snow and directly in the path of a flight lane and at least 10 km from the roosting site.

Three sometimes four flight lanes occurred in the study area. I selected three with the targeted lane having an adjacent lane on either side of it and identified the trajectory of each during preliminary observations. For one lane, I counted the number of birds by positioning myself so that birds flew overhead. To ensure that all the birds were counted, I took up a position that was located at the eastern edge of Wichita before dawn and counted until no birds passed overhead for 10 minutes. A different strategy was used to count the number of birds in the other flight lanes. First, I drove outward in a zig-zag pattern along the trajectory of the flight lane until no crows could be seen in flight or foraging in the fields for two (2.56 km^2) sections (the roads border the edges of a square-mile section). Then, I retraced the

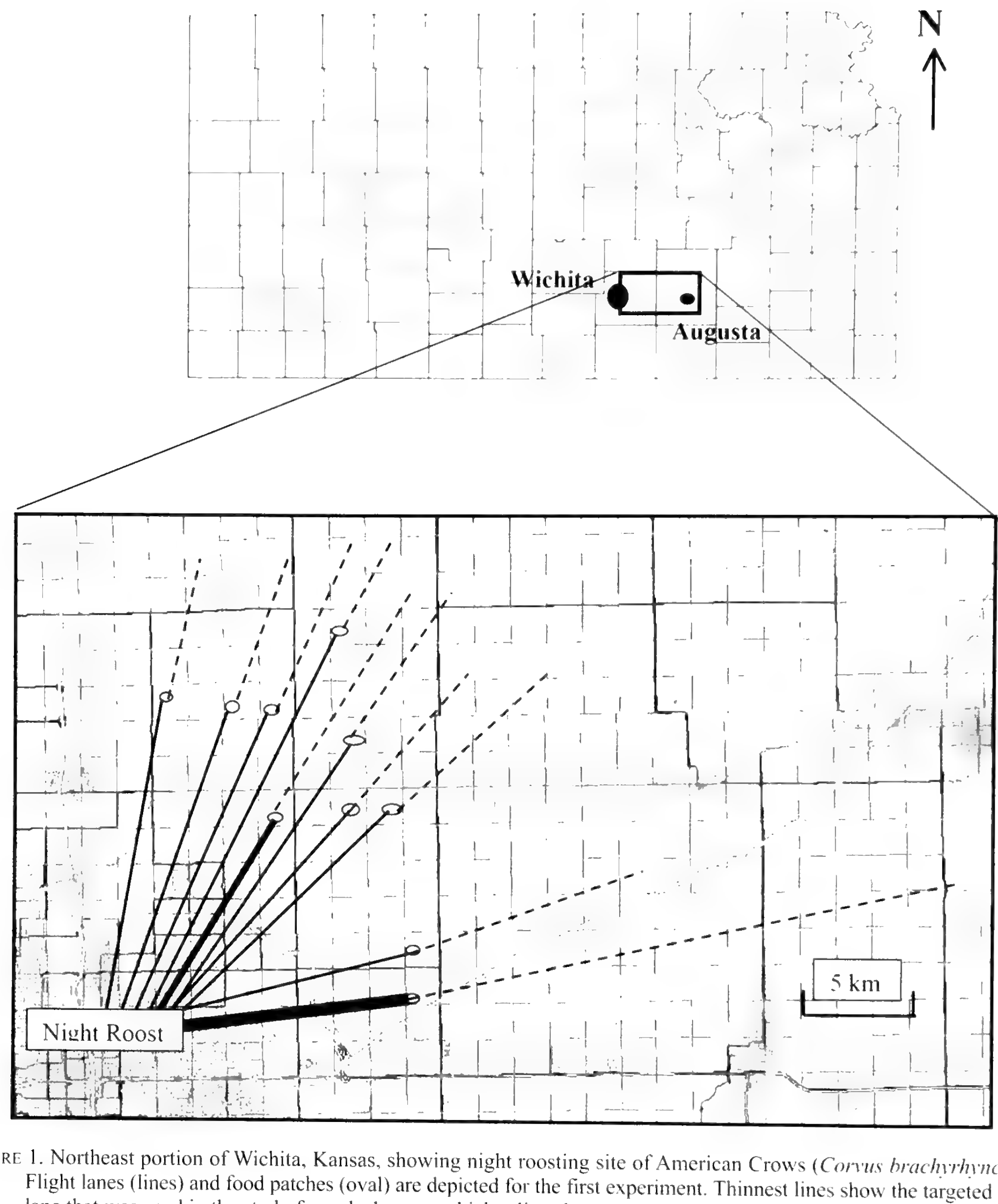

FIGURE 1. Northeast portion of Wichita, Kansas, showing night roosting site of American Crows (*Corvus brachyrhynchos*). Flight lanes (lines) and food patches (oval) are depicted for the first experiment. Thinnest lines show the targeted flight lane that was used in the study for only 1 year; a thicker line shows a lane used for 2 different years; and the thickest line shows a lane that was used for 4 different years. Dashed lines beyond the food patches show where some crows continued to fly and forage.

trajectory of that path counting all crows in the air or foraging. Counting early in the morning and following the trajectory out and back from the night roost reduced the possibility of missing any dispersing crows. Again, all crows were counted until none was observed for two sections. A similar process was repeated for a third flight lane. This counting procedure was conducted for three consecutive mornings before a forecasted snow event. Counting the number using a flight lane as they flew directly overhead had to be done first and was done this way for each flight lane on a different day so that counts were done in similar manner for all 3 flight lanes. The mean counts of those 3 days served as the baseline number of crows using those flight lanes.

On the morning after establishing a food patch, I counted the number of crows passing overhead from a position directly in line with the food patch and between it and the roost until no crows had arrived from the direction of the roost for 20 minutes. After that, I counted the number of crows using the adjacent

flight lanes by tracing the trajectory from the roost and back as was carried out for counting before establishing a food patch. A survey of the crows at the food patch and beyond was conducted after all 3 flight lane counts were completed. These trials were conducted 14 times.

In a second experiment involving 8 trials, food patches were provisioned for 2 consecutive days rather than 1 day as in the first experiment. The change in the number of crows using that flight lane was measured on the third day. In a third experiment, a similar approach and counting procedures were used, but the food patches were offset from the flight lanes. They were placed at a distance of 1.0–1.5 km away from the targeted flight lane. These trials occurred 25 times.

Several non-parametric tests were used to compare differences (Siegel 1956): a Wilcoxon T test was used to compare the number of crows using a flight lane before and after food provisioning; a Mann-Whitney U test was used to compare the counts after 1 or 2 days of provisioning; and a χ^2 test was used to compare the number of discovered food patches placed in or to the side of a flight lane.

Results

More crows used a flight lane after a food patch was set out for 1 day: pre-food, 152 (SD 220) and post-food, 588 (SD 597) (Wilcoxon test, $T = 8$, $n = 14$, $P < 0.02$) (Figure 2). Although in two trials the number of crows using a flight lane decreased after the food patch was set out compared with number of crows using the flight lane beforehand, adverse weather (snow and fog) may have contributed to this decrease. The change in the number of crows using a flight lane ranged from −179 to 1992. In three of these trials, crows were observed veering from an adjacent flight lane to the targeted flight lane. In these cases, the flight lanes merged into one that flew overhead at the counting location.

The number of crows using adjacent flight lanes declined from 1396 (SD 1134) to 1165 (SD 894) after the food patch was discovered (Figure 2), but the difference was not statistically significant (Wilcoxon test, $T = 42$, $n = 14$, $P = 0.66$). The response of crows in adjacent flight lanes veering and joining the targeted flight lane passing over the food patch contributed to the lower mean after the food patch was discovered.

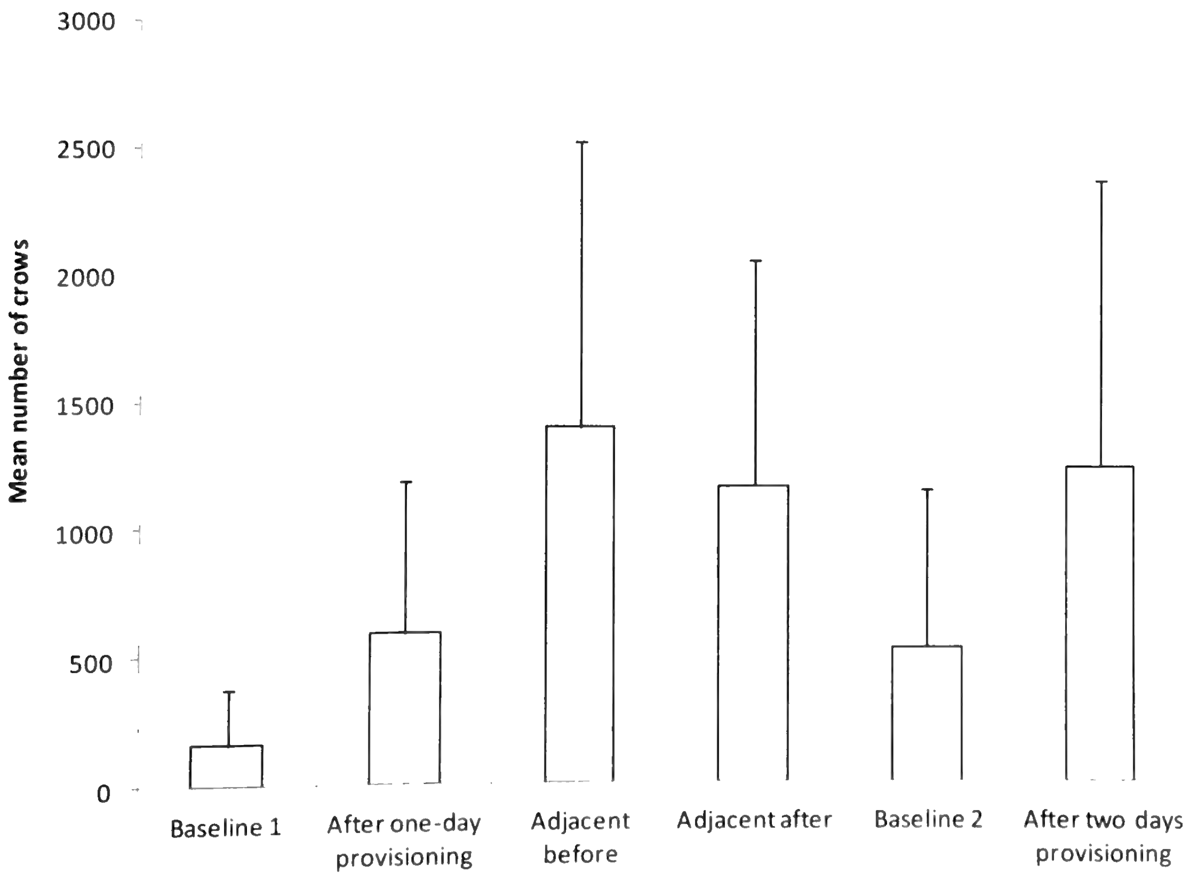

FIGURE 2. Mean number (and standard deviation) of American Crows (*Corvus brachyrhynchos*) in target lane before (baseline 1) and after 1 day of food provisioning, observed in adjacent lanes before and after food provisioning, and in the target lane before (baseline 2) and after 2 days of food provisioning.

When food patches were provisioned for 2 days, the increase in number of crows using the target lane more than doubled from 528 (SD 625) to 1238 (SD 1140) (Wilcoxon test, $T = 0$, $n = 8$, $P < 0.01$) (Figure 2). The number of crows using a flight lane after 2-day provisioning 1238 (SD 1140) was greater than the number after 1-day provisioning 588 (SD 597) (Mann-Whitney U test, $U = 26$, $n_1 = 8$, $n_2 = 14$, $P = 0.02$).

When food patches were offset from the flight lane, different groups of crows discovered some of them. On three occasions, crows from the Wichita roost discovered the food patch as evidenced by the direction from which the birds arrived (trajectory from roost), by their early arrival (0800), and by the increase in the number of birds in these three flight lanes from pre-food 178 (SD 158) to post-food 291 (SD 131). These counts were carried out as in prior experiments. Seven other food patches were found by crows not from the Wichita roost. These crows arrived from a different direction than those from the Wichita roost, at later time (1000) and in fewer numbers (1–10 birds). No other crows were observed in the surrounding area. Of the 25 food patches set to the side of the path of flight lane, 15 were not discovered by any crows the day after provisioning. The proportion of food patches discovered by crows from the Wichita roost when they were placed on the flight lane (12/14) was significantly greater than when they were offset from the flight lane (3/25) ($\chi^2 = 17.6$, $P < 0.001$).

Discussion

The increase in the number of crows using flight lanes where supplementary food had been placed the previous day suggests that information obtained at the roost enabled crows to adjust their foraging behaviour to take advantage of the new food supply. This was especially true when the new food patches occurred in the path of the flight lane and were provisioned for more than 1 day. These data support the hypothesis that night roosts can act as information centres. In this study, the roost was large (>25000 crows) and the number of additional individuals using a flight lane exceeded 1000 on five occasions.

However, the response to discovery of food patch was highly variable, suggesting that additional factors may have influenced the number of crows using a particular flight lane. When a large number of crows responded to the discovery of a food patch, there were too many to access or use the food. Furthermore, most of these crows flew past the food patch, sometimes more than 10 km, suggesting that some were foraging in areas other than the food patch. Although the discovery of a food patch proved to be an attraction, not all arriving individuals necessarily made use of it.

Presumably, the use of flight lanes can be beneficial to crows in more ways than enhancing the discovery of food sources. Vigilance is important while foraging, and flocks can provide an optimal tradeoff between feeding and watching for danger (Ward and Low 1997). When competing for a carcass with a larger raptor, aggregation in flocks ensures success more often for the crows. For example, a flock of American Crows was more successful in displacing a Red-tailed Hawk (*Buteo jamaicensis*) from an animal carcass than a few individuals (Langley 2001).

During this study, crows occurred in three kinds of associations. The most abundant were those in flocks from the Wichita roost. Less common were groups of 2–6 birds that presumably represented territorial family groups not associated with the roost (Knopf and Knopf 1983). A third type observed rarely and intermittently, ranged in size from 10–100 individuals, possibly representing non-breeding crows in the area. Groups of non-breeding crows have been observed near urban areas in California (Caffrey 1992).

Acknowledgements

I wish to thank Alan Maccarone for reviewing the manuscript and the Chickadee Check-off of the Kansas Department of Wildlife for financial support at the start of the project.

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Received 15 November 2013
Accepted 28 January 2014

Muskrat (*Ondatra zibethicus*) Interference with Aquatic Invertebrate Traps

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Cavallaro, Michael C., Anson R. Main, and Christy A. Morrissey. 2014. Muskrat (*Ondatra zibethicus*) interference with aquatic invertebrate traps. Canadian Field-Naturalist 128(2): 200–203.

In field biology, interactions between wildlife and *in situ* equipment occur often. These interactions have the potential to induce a variety of behaviours in local fauna. Here, we note the destructive behaviour exhibited by the Muskrat (*Ondatra zibethicus*) following deployment of aquatic invertebrate traps for research purposes at 12 wetlands located in central Saskatchewan. Of 24 aquatic insect emergence traps used on seven wetlands in our study, 14 (58%) required recurring repairs. In addition, on several occasions, leaf litter bags and their anchoring stakes were torn or chewed. The recurring damage took place in wetlands with Muskrat lodges. We recommend structural modifications to aquatic invertebrate traps in wetland complexes densely inhabited by Muskrats and other semi-aquatic rodents.

Key Words: Muskrat; *Ondatra zibethicus*; aquatic insect emergence traps; destructive behaviour; prairie wetlands; leaf litter bags

When conducting field studies, biologists occasionally encounter unexpected obstacles arising from natural causes, such as adverse weather, and wildlife interference. Overcoming these obstacles can require a substantial amount of time, energy, and resources and, in some cases, may result in gaps in data or a complete loss of data. These experiences may prove to be valuable, and lessons learned can be applied to future experimental design.

As part of a 2013 study monitoring aquatic insect emergence and benthic macroinvertebrate communities in agricultural wetlands located near Alvena, Saskatchewan (52°31'0.12"N, 106°1'0.12"W), we deployed standard aquatic insect emergence traps and leaf litter bags (Merritt *et al.* 1996; Dangles and Malmqvist 2004). Our floating traps covered a surface area of 1 m^2 above the water column. They consisted of a wooden frame supporting mesh-netting sides, with a collection funnel and flask at the top (Figure 1A). Unfortunately, the lower ledge of the frame at the water edge consisted of an 8-cm-wide ledge allowing Muskrats easy access for perching or sitting.

Accounts of Muskrat biology and life history in Saskatchewan are well documented (e.g., Messier *et al.* 1990; Virgl and Messier 1992). Muskrats' diet consists primarily of the roots, shoots, and rhizomes of emergent hydrophytes (Virgl and Messier 1992); occasionally, they will migrate to upland habitat to feed on row crops, especially in agricultural wetlands (Bucci 2009). Other feeding habits include the construction of feeding huts or eating platforms. Built from mud and compacted vegetation, these resemble Muskrat lodges, standing just above the surface of the water (Link 2005*).

In multiple instances, an individual Muskrat or a pair moved building materials, such as mud, dead vegetation, and twigs, onto our traps (Figure 1A); this design allowed the animals to move freely on and off the ledge. No damage to the frame of the traps occurred, but the netting that funneled imago insects was slightly torn. To our knowledge, the only other account of Muskrat interference with aquatic traps is Marcström's (1964) description of Muskrats damaging fish traps in northern Sweden.

We collected emergence trap samples every 3–4 days and repaired damaged nets during these collections. At some locations, Muskrats were directly observed damaging a trap on multiple occasions, and this prompted modification of the traps. Subsequently, chicken wire, 2.5-cm mesh (Cable Ben-Mor, Model #94002; Rona, Boucherville, Quebec), was fastened around the outside of the traps and across the bottom to protect the netting.

We acknowledge that the addition of chicken wire mesh structure below the floating trap could have an influence on emerging insects, as several aquatic insect taxa, such as Odonata, require substrate (e.g., emergent vegetation) to achieve the final stage of metamorphosis (Merritt *et al.* 1996). Our placement of emergence traps focused on both open water and emergent vegetation habitats and the method for anchoring each trap was identical. Samples collected from emergence traps — with or without chicken wire — in open water habitats did not contain an overabundance of taxa that require substrate. Also, frequent collection of samples allowed for direct observation of potential bias by searching for insect exuviae attached to the emergence traps. A bias in sampling could be inferred by an overabundance of insect exuviae from substrate emerging insects.

Several times, we observed Muskrats seeking refuge under the emergence traps even after modification.

However, the addition of chicken wire under the trap prevented them from surfacing inside the trap, effectively preventing damage (Figure 1B). Adult Muskrats were unable to enter the trap, although a single juvenile Muskrat was observed moving freely over the side of the chicken wire. This same juvenile collected senesced wetland vegetation to create a resting area (Figure 1C). In addition to nesting materials, fresh vegetation was also found on the traps. With a variety of potential predators in the area (e.g., Coyotes, *Canis latrans*; Red-tailed Hawks, *Buteo jamaicensis*; and humans), this suggests that the floating traps provided a safe vantage point to feed.

We assembled leaf litter bags to monitor shifts in benthic macroinvertebrate communities throughout the growing season. Roughly 10 g of dried leaf litter from senesced native wetland vegetation (e.g., Broadleaf Cattail, *Typha latifolia*) were added to a mesh bag. The bags were anchored in the sediment with 1-m spruce stakes. On multiple occasions, while removing leaf litter bags during the course of our experiment, we observed teeth marks on the spruce stakes (Figure 1D). On four instances during early spring, we found evidence of Muskrats chewing open the leaf litter bags. We are uncertain why they did this, as there was no evidence of them feeding on the contents.

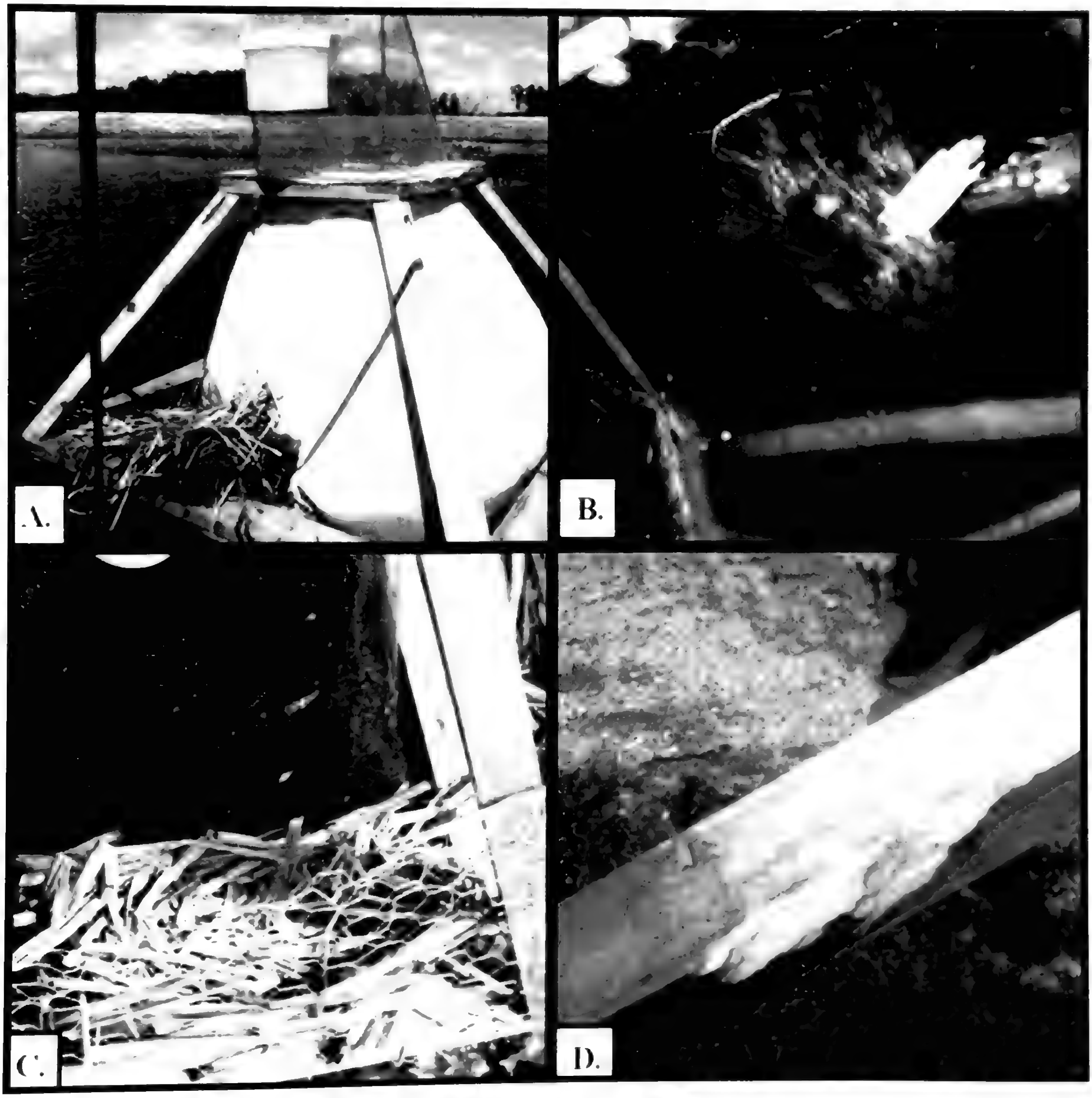

FIGURE 1. (A) Aquatic insect emergence trap (1 m × 1 m) with Muskrat (*Ondatra zibethicus*) building material on its lower ledge. (B) Juvenile Muskrat seeking refuge under an aquatic insect emergence trap. (C) Aquatic insect emergence trap after chicken wire was installed. In this photo, the chicken wire is bent from the juvenile Muskrat moving on and off the trap. (D) Spruce stakes used to anchor the leaf litter bags showing teeth marks and evidence of chewing.

Muskrats display strong territorial behaviour during breeding season; their aggressive behaviour reaches a peak from late April to late May and diminishes in early June (Beer and Meyer 1951). The frequency of our trap repairs was highest from late May into early June, when we suspect invasion of the territory by conspecifics prompted destructive territorial behaviour. Some Muskrats were noticeably agitated by our presence; individual animals were observed sitting on their lodges and chattering their teeth or emitting a sharp, whining noise. Mizelle (1935) recounts observations of swimming muskrats "clapping" their fanned tails on the surface of the water when startled. Other semiaquatic rodents are described as displaying defensive behaviour that involves hissing, whining, or gnashing their teeth toward other individuals (Leighton 1933).

In the absence of aquatic or semiaquatic plants, overwintering Muskrats are known to consume woody material such as tree bark (Lewis *et al.* 2000). The late spring–summer transition that occurred in 2013, our study year, did not support wetland vegetation growth until late May. During winter and early spring, Muskrats do not store food reserves and are confined to foraging beneath the ice (Virgl and Messier 1992). With the lack of available food resources within the wetlands and upland habitat, spruce stakes placed in the wetland flowing ice melt could serve as an easy source of nutrients. However, the leaf litter bags were constructed with nylon and fibreglass mesh (0.25–1 mm), with no apparent nutritional value. Muskrats exhibit feeding plasticity, consuming diverse food items and allowing them to occupy a variety of aquatic ecosystems (Bucci 2009). Like most rodents, they must chew regularly to wear their teeth adequately (Lewis *et al.* 2000). Dental wear in Muskrats is primarily driven by diet and life history strategies — burrowing versus lodging (Lewis *et al.* 2002). Muskrats with varying life history strategies may require greater dental wearing from other activities (e.g., chewing or gnawing woody materials). The dominant plant species at each wetland in our study area, a non-woody monocot, Broadleaf Cattail, might not have been sufficient to achieve dental wearing, which might explain why Muskrats gnawed our stakes and leaf litter bags (Figure 1D).

The spring snow melt in 2013 caused severe flooding throughout Saskatchewan. Reports indicated that, at the height of the flooding, the South Saskatchewan River rose 1.5 m (Water Security Agency 2013*). As a direct effect of this flooding, Muskrats were able to occupy new habitats and move freely throughout their known range. Our field sites in Alvena, Saskatchewan, were roughly 5.5 km from the South Saskatchewan River; thus, flooding may have contributed to a high influx of Muskrats in our study area (F. Messier, University of Saskatchewan Biology Department, August 2013, personal communication).

Based on our experience over the season, we recommend modification of aquatic emergence traps to include a narrower, or nonexistent, perching ledge at the bottom. Where funds are insufficient to construct new traps, shielding the netting and bottom of the traps with chicken wire is effective (Figure 2). As a measure of caution, and to be certain Muskrats cannot gain access to the trap, chicken wire should be firmly attached to all sides and bottom. To prevent damage to leaf litter bags, encasing them in a rigid mesh structure with galvanized wire would fix them to a desirable location, provide protection from Muskrats, and act as a suitable alternative to anchoring with stakes; this strategy could be used in both lotic and lentic freshwater systems. Galvanized wire mesh has been used to protect the soil–surface water interface bordering dams, dikes, canals, and shoreline property from Muskrat burrowing and many state agencies in the United States document these methods in external reports (e.g., Link 2005*). As a final level of precaution, surveys should be conducted to determine whether Muskrats are present before invertebrate traps are installed in wetlands so that modification may be made to protect the traps appropriately. However, because Muskrat lodges are not always apparent, as they are typically hidden within dense emergent vegetation, trap modifications may be made as a preventive measure.

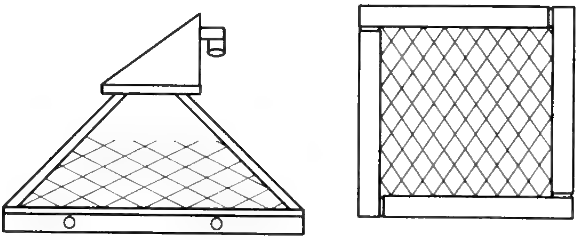

FIGURE 2. Emergence trap with chicken wire fixed to sides and bottom to prevent Muskrat (*Ondatra zibethicus*) entry and damage.

In conclusion, the high Muskrat density in our study area resulted in substantial additional work and time spent during the field season, especially during peak Muskrat breeding season (late April to late May). We hope the advice in this note helps field biologists, entomologists, and wetland scientists planning and executing aquatic invertebrate experiments in habitats occupied by Muskrats or other semi-aquatic rodents, such as beavers.

Acknowledgements

We thank T. Gallagher, K. Majewski, and A. Zahara for field assistance. In addition, R. Clark, N. Michel, and D. Oswin provided helpful revisions and suggested emergence trap modifications. A grant to C. A. Morrissey from the Natural Sciences and Engineering Research Council of Canada supported this research.

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Received 19 November 2013
Accepted 4 January 2014

Pygmy Shrew (*Sorex hoyi*) in Montana East of the Rocky Mountains with Comments on its Distribution across the Northern Great Plains

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Hendricks, Paul, and Susan Lenard. 2014. Pygmy Shrew (*Sorex hoyi*) in Montana east of the Rocky Mountains with comments on its distribution across the northern Great Plains. Canadian Field-Naturalist 128(2): 204–206.

Range maps for Pygmy Shrew (*Sorex hoyi*) show a large hiatus over much of the northern Great Plains between the Rocky Mountains and eastern North Dakota. We report a new record of the Pygmy Shrew in northeastern Montana, review previous records for the state and adjacent regions bordering Montana to the north and east, and suggest that the range boundary in the northern Great Plains be redrawn farther south to include all of Montana north of the Missouri River. This is consistent with the known range of the Pygmy Shrew in eastern North Dakota and South Dakota, where the species has been documented only north and east of the Missouri River, although records are still lacking from north of the Missouri River in northwestern North Dakota and adjacent regions of Canada. Pygmy Shrews will probably be found at additional localities in prairie regions of Canada adjacent to Montana, most likely in association with prairie pothole wetlands, river bottom riparian vegetation, and hardwood draws.

Key Words: distribution; Montana; northern Great Plains; prairie potholes; Pygmy Shrew; *Sorex hoyi*; shrews; habitat

The Pygmy Shrew (*Sorex hoyi*) occurs across boreal and subarctic North America, with populations in the United States also extending south along the Rocky Mountains in the west and the Appalachian Mountains in the east (Long 1974; Diersing 1980; Hall 1981). Pygmy Shrews occur in a variety of microhabitats, such as bogs, marshes, dry grassy clearings, mesic forested habitats, and associated riparian corridors (Long 1974; van Zyll de Jong 1983).

In Montana, Pygmy Shrews were first reported in 1937 from the Rocky Mountain region in the western third of the state (Koford 1938), and most additional specimens have been reported west of or near the continental divide (Setzer 1952; Hoffmann *et al.* 1969; Key 1979; Foresman 1999). More than 150 individuals have been captured at about 29 locations in Montana over at least 160 000 pitfall trap–nights (Hoffmann *et al.* 1969; Allen *et al.* 1997; Foresman 1999; Carson *et al.* 2006*; Dorak *et al.* 2012*), indicating that Pygmy Shrews may be relatively common at some locations, but uncommon to rare over much of their range within the state. In montane western Montana, Pygmy Shrews tend to occupy mesic sites in a variety of habitats typical of other portions of their North American range; these include sagebrush, riparian areas, marshy or boggy sites, and most coniferous forest types except those at the highest elevations (Foresman 1999, 2012).

Most distribution maps for the Pygmy Shrew show a large hiatus in the southern part of its range that projects northward between the Rocky Mountains of western Montana and southern Alberta in the west to eastern North Dakota and South Dakota in the east (Long 1974; Diersing 1980; Hall 1981; van Zyll de Jong 1983; Naughton 2012). This is consistent with the characterization of the Pygmy Shrew as a species with boreal and montane affinities (Hoffmann and Jones 1970; Jones *et al.* 1983). Thus, the Pygmy Shrew is inferred to be absent from most prairie regions of the northern Great Plains east of the Rocky Mountains. In this note, we describe a new specimen of Pygmy Shrew captured in the prairie region of eastern Montana and discuss this finding in the context of previous records of the species from the northern Great Plains.

On 11 September 2012, we captured a female Pygmy Shrew in a Museum Special snap trap (Woodstream Corp., Lititz, Pennsylvania, USA) from a trap line set in a stringer of riparian Eastern Cottonwood (*Populus deltoides*) adjacent to an irrigation canal 2.9 km north of the Missouri River (48°3'36"N, 106°14'16.79"W, 622 m elevation), 10.5 km southeast of Nashua, Valley County, Montana (Figure 1, site 4). The line consisted of single snap traps baited with peanut butter and Sherman live traps (H. B. Sherman Inc., Tallahassee, Florida, USA) baited with rolled oats and bird seed at 10 stations. The specimen was prepared as a study skin (UMZM 20382; museum acronyms follow the Global Registry of Biodiversity Repositories [http://grbio.org]) and deposited in the University of Montana, Philip L. Wright Zoological Museum. This was the only Pygmy Shrew captured during 940 trap-nights of effort at 46 sites. It was the first record of the species from Valley County and the fifth specimen reported in Montana from prairie regions east of the Rocky Mountains. Also captured in this trap line were Deer Mice (*Peromyscus maniculatus*) and White-footed Mice (*P. leucopus*).

Pygmy Shrew specimens previously found in eastern Montana (Figure 1, sites 1–3) have been associated with mostly treeless prairie pothole regions north of the Missouri River. The first record (site 1) was a female

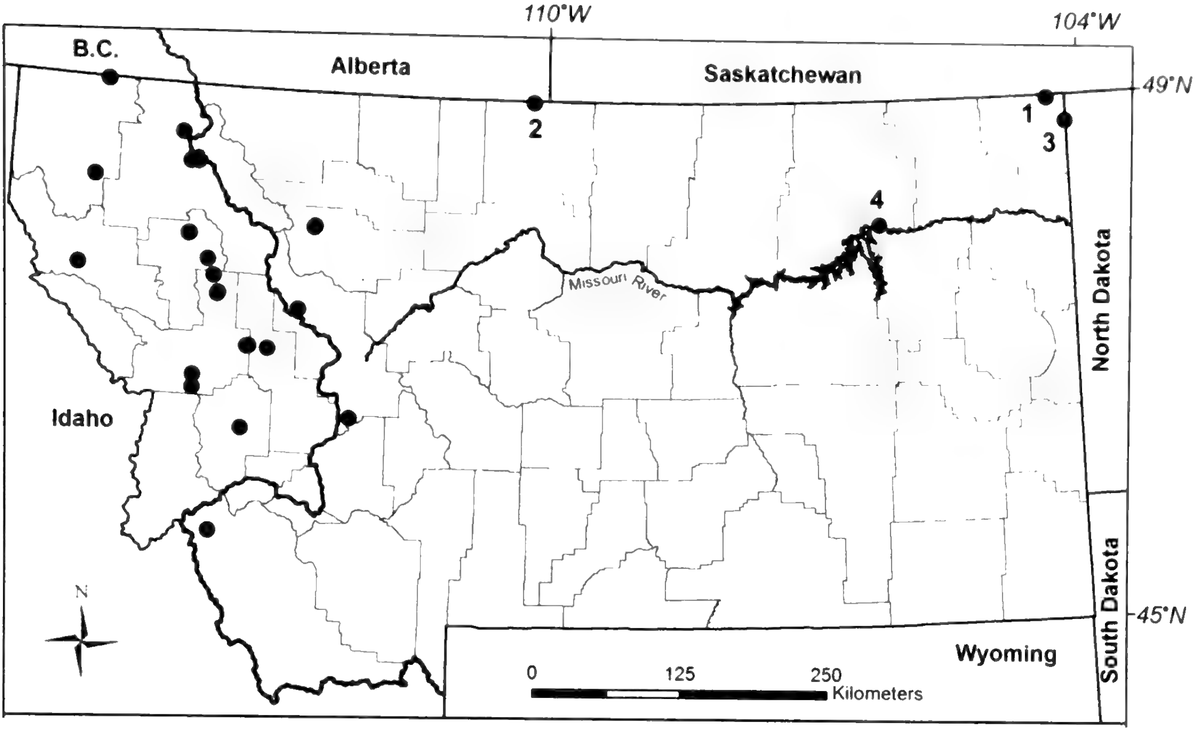

FIGURE 1. Distribution of Pygmy Shrew (*Sorex hoyi*) in Montana. Numbered sites are locations where Pygmy Shrews have been found in prairie regions of the northern Great Plains: (1) Widgeon Slough, Sheridan County; (2) Wild Horse Lake, Hill County; (3) Goose Lake, Sheridan County; (4) 10.5 km southeast of Nashua, Valley County. Sources for unnumbered locations are Koford (1938), Setzer (1952), Hoffmann *et al.* (1969), Key (1979), Foresman (1999), and specimens in the University of Montana, Philip L. Wright Zoological Museum (UMZM). The continental divide is shown in bold.

(UMZM 19026) captured by Dennis Flath and John Ciralli in a snap trap on 23 July 1977 near Widgeon Slough (48°58'22.79"N, 104°15'7.19"W, 663 m elevation) in Sheridan County, about 170 km east of the Valley County site. The second record (site 2) was a partial skull (UMZM 18672) recovered from a raptor pellet on 20 July 2000 near Sage Creek at Wild Horse Lake (48°59'5.99"N, 110°10'26.4"W, 853 m elevation) in Hill County, about 315 km west of the Valley County site (Hendricks 2001). The third record (site 3) included two unsexed individuals (UMZM 20394, the other specimen misplaced) captured by Jenny Flesch in a pitfall trap and a snap trap at one trap station on 22 August 2005 in a marshy area near Goose Lake (48°47'31.2"N, 104°2'56.4"W, 625 m elevation) in Sheridan County, also about 170 km east of the Valley County site.

Although few in number, the distribution of Pygmy Shrew records from eastern Montana suggests that this species is widely distributed across the northern Great Plains in Montana north of the Missouri River, but in localized wetland and riparian habitats. Extensive small-mammal trapping throughout eastern Montana south of the Missouri River (Lampe *et al.* 1974; Matthews and Swenson 1982; Carson *et al.* 2006*; Dorak *et al.* 2012*) has resulted in no additional records for this shrew species. We suggest that future range maps for the Pygmy Shrew in Montana include the entire region north of the Missouri River.

The southern border that we propose for the range of the Pygmy Shrew across the northern Great Plains appears to match, more or less, the maximum extent of the Laurentide ice sheet during the late Pleistocene (Clayton and Moran 1982). This distribution of the Pygmy Shrew in eastern Montana is also consistent with documented locations in the eastern half of North Dakota and eastern South Dakota, where the species has been found only north and east of the Missouri River (Long 1974; Hall 1981; Jones *et al.* 1983; Higgins *et al.* 2002), often in association with marshy prairie potholes and lakeshores and Green Ash (*Fraxinus pennsylvanica*) hardwood draws (Gruebele and Steuter 1988; Backlund 1995) in formerly glaciated regions of the Drift Plains and Missouri Coteau. We expect that Pygmy Shrews will be found at additional locations in eastern Montana and adjacent prairie regions north of the Missouri River in Canada and northwestern North Dakota as more surveys are undertaken for shrews in appropriate wetland, hardwood draw, and riparian habitats in this area of the northern Great Plains.

Acknowledgements

Our small-mammal surveys in northeastern Montana were part of a larger vertebrate survey conducted for the Assiniboine and Sioux Tribes of the Fort Peck Indian Reservation, funded under Tribal Government Resolution 26-571-2012-03. We thank Jeanne Spaur of the tribal government for soliciting and coordinating the funding of our survey, which was managed through the auspices of the Montana Natural Heritage Program. We are most grateful to Claudine Tobalske of the Montana Natural Heritage Program for producing the map. An earlier draft of our paper benefited from the comments of two anonymous reviewers. All vouchers are deposited in the Philip L. Wright Zoological Museum (UMZM), University of Montana, Missoula.

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Received 4 January 2014
Accepted 29 January 2014

Book Reviews

Book Review Editor's Note: We are continuing to use the current currency codes. Thus Canadian dollars are CAD, U.S. dollars are USD, Euros are EUR, China Yuan Remimbi are CNY, Australian dollars are AUD and so on.

Zoology

Animals of the Serengeti and Ngorongoro Conservation Area

By Adam S. Kennedy, and Vicki Kennedy. 2014. Princeton University Press, 41 William Street, Princeton, NJ, USA, 08540-5237. 152 pages, 18.50 USD, Paper.

Birds of the Serengeti and Ngorongoro Conservation Area

By Adam S. Kennedy. 2014. Princeton University Press, 41 William Street, Princeton, New Jersey, USA, 08540-5237. 224 pages, 18.50 USD, Paper.

The Serengeti-Mara ecosystem is world-renowned for its massive herds of migratory wildebeest, zebra, and other grazers, encompassing approximately 25,000 km^2 of northern Tanzania and adjacent Kenya. The bulk of the ecosystem lies within Serengeti National Park and the Ngorongoro Conservation Area and adjacent game reserves, with the remainder in the Maasai Mara of Kenya. Immediately to the south of the Serengeti ecosystem are the Ngorongoro Highlands including the famous Ngorongoro Crater. Following up on the 2012 success of their guides on the animals and birds of the Maasai Mara, the Kennedy's have recently released *Wildlife of the Serengeti and Ngorongoro Conservation Area* and *Birds of the Serengeti and Ngorongoro Conservation Area*. Former safari camp managers and now professional guides, Adam Scott Kennedy and his wife Vicky bring their photographic talents, experience, and first-hand knowledge of the Serengeti, Ngorongoro, and surrounding areas together in this new pair of field guides. Although these two new field guides enter a relatively crowded market, there is a niche for them, particularly for visitors on their first East African safari.

Animals of the Serengeti and Ngorongoro Conservation Area is a bit of a misnomer since it only treats mammals and a few reptiles, with birds in a separate volume and nothing at all on amphibians, fish, or invertebrates. It does cover 70 mammal species, including most of the species likely to be encountered on safari in Serengeti and Ngorongoro, or for that matter elsewhere on Tanzania's "Northern Circuit". A notable exception is the Oryx, which was has been observed just east of Serengeti National Park in the Loliondo area near Lake Natron. The guide also excludes bats, shrews, and most of the 40 or so species of rodents known from the Serengeti. No great loss, for although important components of the ecosystem, these small mammal groups are difficult to see and even harder to identify when not in the hand. The *Animals* field guide also covers 18 of the reptiles most likely to be observed on safari or near Serengeti area lodges. It includes such obvious choices as Nile Crocodiles and Black Mambas, but also brightly-coloured agamas and nocturnal geckos. Surprisingly, neither the Pancake Tortoise nor the Egyptian Cobra were included, both striking species that I have seen by day in the Serengeti.

The guide is focussed on the Greater Serengeti area and has a brief introductory section with maps and text on the general geography and ecology of the area, including the great migration, as well as suggested locales for great wildlife viewing. While I might quibble with some of the details, the authors have done an admirable job distilling this information into a concise introduction that I think it will help visitors place what they see into a larger ecosystem context and ultimately deepen their appreciation.

The guide is packed with 146 colour photos, showing both males and females for sexually dimorphic species, and even young where space permits. In addition to great photographs, what sets this guide apart from many traditional field guides is the light and accessible tone of the text. Each species has a half-page to 4-page treatment, with information on identification, preferred habitat, diet, and habits. Although total length and shoulder height are provided, I do wish that average weight (or a range) was also provided for each mammal species. For better-known species, there are interesting notes on their distribution in the Serengeti and Ngorongoro, as well juicy tidbits on their ecology or behaviour. For example, the reader is warned of the honey badger's tendency to go for the genitals when confronting humans. Perhaps apocryphal, it makes for good reading nonetheless and is a part of safari lore. The guide also has informative sidebars with insight and observations provided by local Tanzanian guides, the "Super Six". It is a bit like having an experienced flesh-and-blood guide along with you.

Common and scientific names used in the guide generally follow those used by IUCN, and alternative names typically provided where necessary to avoid confusion. Welcome additions included for each species are the Kiswahili and Maasai names (good luck with the pronunciation!), and the etymology for some of the more interesting names is also provided. The species are presented in a "simple order" whose underlying rationale escapes me, and I think standard taxonomic order would have been preferable. Fortunately, there is a detailed Table of Contents listing all species, as well as both a detailed and a short index at the back, so it isn't difficult to find a particular species.

Although some may prefer to read it back home, this field guide is compact and light enough (14 × 21 cm and only 320 g) to bring on safari. Wildlife sightings are often fleeting, in poor light, or obscured by vegetation, so having a field guide handy to confirm identification is helpful, particularly for lesser-known species. Even if you don't pull out it out while on game drives, having the guide handy to refer to in the evening or other down time will help reinforce the names of unfamiliar species observed during the day. If you are particularly keen about herps, I would also recommend getting a copy of Spawls *et al.*'s 2006 *Reptiles and Amphibians of East Africa* (240 pages) that covers 230 of the more commonly encountered species reptile and amphibian species.

With over 500 documented species, Serengeti National Park and the Ngorongoro Conservation Area are recognized as Important Bird Areas by Birdlife International, and the Serengeti Plains are also an Endemic Bird Area. Novice birders may find this diversity daunting, and traditional field guides covering all of East Africa, with 600 pages and 1400+ species, can be overwhelming. Adam Scott Kennedy's *Birds of the Serengeti and Ngorongoro Conservation Area* is intended to make this area's birdlife more accessible by using photographs and limiting the guide to 264 of the more commonly observed species. I was surprised by several omissions such as the spectacular Southern Red Bishop and the endemic Grey-crested Helmet-shrike, and was puzzled by the inclusion of a sidebar on the Dodo. Fortunately, it makes note of the endemic Fischer's Lovebird, Usambiro Barbet, Grey-breasted Spurfowl, and Rufous-tailed Weaver, which are relatively easy to find in the Serengeti.

The book is arranged by nine "habitats", with birds typically found in a particular habitat grouped together, rather than by standard taxonomic order as in most field guides. The habitats are described in the introduction and include: plains; marsh & water; woodland scrub & garden; acacia scrub; village birds; forest & crater highland; air; night; and Lake Victoria specials. The intent is to help novices more rapidly locate the likely bird species in the guide based on where it is observed. This approach has its limitations due to poorly defined or overlapping habitats, especially for widely distributed species such as the Grosbeak (Thick-billed) Weaver, which was included as a "Lake Victoria Special" but is also found in the Ngorongoro highlands and beyond. I also found it frustrating, for example, to have the hornbills spread out on pages 37, 119, 169, and 183. Fortunately, the habitats are colour-coded in the guide, and there are numerous cross-references to similar-looking species that may occur in other habitats.

The quality of the photographs is truly impressive, as is the artistic and technical skill evident in the layout. There are typically 2-3 species per page (with full page accounts for some of the more charismatic or spectacular species), and the backgrounds of the numerous images are seamlessly blended, so that it often appears as if birds were actually side by side in their natural habitat. Both sexes are often shown, and even some immatures. The informative and accessible species' accounts have tips on identification and similar species, and touch upon distinctive songs or calls, behaviour, ecology, and other points of interest. Scientific names are not provided in the main text (they are in an index at the back), but most novice birders often have a hard enough time remembering the common name, let alone the Latin one. KiSwahili names are sadly not provided (Helmeted Guineafowl the lone exception), but perhaps should have been, at least for the more distinctive species such as the Ostrich and vultures. Although it is not a bird-*finding* guide, a bit more information on local distribution/abundance or particular birding "hot-spots" would also have been appreciated. For example, the cliffs of Olkarien Gorge at the eastern edge of the ecosystem are well-known (at least in some circles) as a critical nesting site for Rüppell's Vultures.

This field guide is "aimed at all levels of birding ability" and it is definitely suitable for novice birders and for those on a safari primarily for mammals and larger wildlife. The guide only covers about half of the species known from the Serengeti and Ngorongoro Conservation Area, so keen birders will likely want to bring a more comprehensive field guide on their trip. Nonetheless, the quality of the photographs and text would make it a fine addition to field naturalist's library with an interest in East Africa.

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Rare Birds of North America

By Steve N. G. Howell, Ian Lewington, and Will Russell. 2013. Princeton University Press, 41 William Street, Princeton, NJ, USA, 08540-5237. 448 pages, 35.00 USD, Cloth.

The avid lister will need to wear a bib for this book as it contains all the species they will drool over. The authors include all the species seen in North America five times or less since the 1950s. These are the real rarities or "mega-ticks" that move the combat birders to drive for hours to add them to their lists.

Rarities come at us from three directions. Some sweep in on winds from Europe, others overrun their territory from the south and some blow over from eastern rim of Asia. Not surprisingly the east coast (Newfoundland to Maine), the states that border Mexico and Alaska's outer islands account for a high proportion of these strays. Record committees have to evaluate new sightings, taking in to account the bird's migratory tendencies, records of movements in other countries as well as the evidence provided by the observer. For example, if a European finch is found in Newfoundland, the committee will consider if the species has a history of wandering, is it being seen in Iceland or Greenland and is it a popular cage bird. The authors have taken all the accepted rarity records to 2011 plus a few later sightings. For this book the authors have stretched these limits and include some species that have questionable provenance, yet may be true records for a coverage of 262 species. For example, the authors discuss the records of the Common Shelduck, a bird usually dismissed as an escapee by the ABA, on the grounds that it is possible some may be true vagrants. They do not include species that breed annually even though they may be vagrants for most of the continent (Eastern Yellow Wagtail). The book has a North American focus so it does not include many rare Canadian birds (such as Thick-billed Kingbird) as these are frequently inhabitants of the southern States.

Before reading the species accounts the buyer needs to read the introduction, as it contains much thought-provoking information. There are discussions on migration and vagrancy, the influence of weather, mis-orientation and disorientation and dispersal. The authors introduce the concept of false vagrancy – birds that are rarely seen but are probably regularly occurring species (European Storm Petrel, Red-footed Booby). These birds are in areas that simply lack coverage. The introduction also covers topography moult and aging; complex topics that need to be considered for any vagrant.

I was surprised by the author's use of Light-mantled Sooty Albatross instead of the currently accepted Light-mantled Albatross (*Phoebetria palpebrata*). They also include the Eurasian Hen Harrier (*Circus cyaneus*) as a separate species to the Northern Harrier *(Circus [cyaneus] husonicus*), a split I have not seen accepted elsewhere. (Although I have always thought they were different species, based on their behaviour). There is an error in the index for Little Shearwater as the quoted page 98 is devoted to paintings of *Thalassarche* albatrosses.

The book is beautifully illustrated by Ian Lewington. The paintings are technically accurate, but also capture the specie's attitude effectively. For example, Lewington catches the funny, hunched posture of swallows, the perky look of a Hoopoe and the grace of the frigatebirds. Most birds are shown in different positions or plumages as appropriate. The artist frequently includes common, look-alike species (like Common and Spotted Sandpipers, Little and Snowy Egret). I have seen about half of the birds in this book, just not in North America. So I really enjoyed looking at illustrations as they evoked pleasant memories. This alone made the book worthwhile for me.

One of my most recent lifers was the Himalayan Bluetail or Orange-flanked Bush-robin. The vagrant listed in this book is the Red-flanked Bluetail once considered a subspecies *Tarsiger c. cyanurus* breeding in northern Asia with *T. c. rufilatus* breeding in the Himalayas. The Himalayan Bluetail is now considered by some as *T. rufilatus*, a distinct species. Given the aggressive attention to detail by records committees as carried into this book I was surprised not to see this possibility considered. The more northern Red-flanked Bluetail, if accepted as a split, is a long distance migrant rather than a short-distance altitudinal migrant so it is the more likely vagrant. The plates are lovely though and they did bring up my views of this pretty little bird along the roads around Darjeeling.

Clearly this is a must buy book for the passionate list keepers, particularly those who are strongly competitive. But there are good reasons for the rest of us owning this book. When examining the details for a rare species the authors need to consider the differences to common birds. For example, separating the European Storm Petrel from the more abundant Wilson's Storm-petrel. These careful comparisons teach me points of identification that I have overlooked for years. I await the return of our American Coots so I can check the under-tail coverts, something I have never done on the thousands of coots I have seen. I will look for the pale orange bill base on the Green-winged Teal (My photo of a male does not show this, but it may be the angle. I searched the net images and this is a very, very difficult to see field mark. Good luck if you find a vagrant Garganey). I will look for the black mark at the base of the wings of a Great Blue Heron. Maybe I will be able to see the plain primaries on an American Woodcock if I use a better flashlight. It is an education of field observation just to read this book. It is great value for the price and a highly recommended purchase for all birders.

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Deer

By John Fletcher. 2014. Reaktion Books Ltd., 33 Great Sutton Street, London, UK, EC1V 0DX. 207 pages, 19.95 USD, Paper.

As I read author John Fletcher's book, *Deer*, I couldn't help but thinking of some of the deer that I have seen in my lifetime. White-tailed deer are over-abundant throughout much of Northeast U.S., but interestingly, not particularly common where I live (Cape Cod, Massachusetts), so encounters are especially memorable. My son and I commonly position our trail-cam in different places to try and capture pictures of the elusive white-tailed deer among other animals such as eastern coyotes/coywolves, fishers, and otters inhabiting Cape Cod. I have fond memories of seeing a white-tailed buck in a clear-cut stand and moose in ponds in the White Mountain National Forest, New Hampshire on family camping trips; moose in Baxter State Park Maine is where my son saw his first wild moose; Yellowstone National Park introduced me to mule deer and elk (or wapiti as Fletcher refers to them to not confuse them with moose since *Alces alces* is called elk in the Old World), as well as bison, pronghorn, bighorn sheep, and mountain goats, ungulates that are related to deer. Although my professional interest involves studying predators, mainly coywolves, I am always interested in seeing and learning about the various deer species that I encounter.

The back cover of Fletcher's book introduces the reader to his book and is worth quoting here: "The Celts called them "fairy cattle" and the Greeks associated them with the hunter goddess Artemis, but for most people today, deer are seen as cute, like Bambi, or noble, like the Monarch of the Glen. They can be a danger when we're driving at night, or they can simply be a tasty venison burger. But while we may not often eat humble pie—an actual pie filled with deer organs—deer still appear in religion and mythology, on coats of arms, in fine art, and in literature ranging from *The Yearling* to *Harry Potter* and *The Chronicles of Narnia*. In *Deer*, veterinarian and deer farmer John Fletcher brings together the cultural and natural history of these dignified animals. Fletcher traces the evolution of deer, explaining why deer grow and cast aside their antlers each year and describing their symbolism in various cultures throughout history. He divulges the true story of Rudolph and Santa's other reindeer and explores the role deer have played as prized objects of the hunt in Europe, Asia, and America. Wide-ranging and richly illustrated, *Deer* provides a fresh perspective on this graceful, powerful animal that will appeal to hunters and gatherers alike."

The above description accurately articulated the meaning of the book and what I learned from it. The book is well illustrated with 93 pictures, 66 of those in colour. Fletcher introduces the 40 species of wild deer (including elk/red deer, moose, roe deer, white-tailed deer, and caribou/reindeer), or Cervidae family, found throughout the world. Fletcher makes it clear that there are many kind of deer (like moose) even if they aren't the proto-typical "deer", such as the white-tailed deer in North America. The first chapter provides a good taxonomic introduction to both Old and New World deer. While Fletcher divides them into the two regions it can be a little confusing as some species such as elk/wapiti, *Cervus elaphus* (meaning pale-coloured rump by Native Americans; note this same species is called red deer in Europe) and North American moose (confusingly called elk in the Old World) occur circumpolar. That being said, the first chapter does a good job of introducing the cast of characters of the book, with red deer being the species most often referred to throughout the text.

In the introduction, Fletcher noted that the book is a cross fertilization between science and the arts. That was certainly the case as the book mostly focussed on human uses of and interactions with deer. I learned some interesting things such as: (1) grazers are generally gregarious and are adapted to resist high infestations of parasites whereas browsers concentrate their food and have little ability to combat them; (2) deer are strongly linked to human symbolism such as regeneration (i.e., males re-growing a set of antlers each year), renewal, power, longevity, royalty, and justice; (3) many of the early "noble" people of the Old World (e.g., kings/queens) were associated with romantic images of deer, such as putting collars on wild red deer stags with inscriptions like the date and person putting the collar on the deer (those collars would later be retrieved by others who saw the message from the royalty that inscribed them); (4) there is a close association between the legends of Robin Hood and deer such that he and his comrades would steal/poach deer from the rich to feed the poor, and this scene is in every movie on the subject; (5) red deer imported to New Zealand have become the first domesticated livestock in 5,000 years; and (6) many deer species will eat meat if given the chance. My favourite quote from the book came on page 61 when Fletcher referred to the image of deer as "ephemeral wild animals briefly glimpsed which contributes to their mystery and allure, fuelling their symbolic role."

John Fletcher lives in Scotland where he runs a deer farm, which is a private estate with an enclosed deer herd living within its confines. His background and location clearly influenced the book as it was heavily biased toward Old World (Europe) deer species. In fact, in chapter 1, where he provided an introduction to the family of deer, the Old World species were discussed three times more than the New World deer (about 15 versus 5 pages). Furthermore, many of his accounts of cultural symbolism, such as converting deer into sha-

mans, came from Old World examples and much less from the New World. At times I had difficulty following the many places and names (especially kings, queens, and other royalty) to which Fletcher discussed. This probably isn't too surprising since I have lived in the United States my entire life and find the whole concept of nobility and classification of different classes of people bizarre, and almost imaginative (e.g., "George Walpole, third Earl of Orford"). On page 142, Fletcher even acknowledged the complexity of symbolism by noting, "For us in the twenty-first century, the world of medieval and Renaissance symbolism seems esoteric and confusing." Even though many of the passages from the book were intended for or likely to be understood by only a small number of people with a specialized knowledge or interest, the thoroughly illustrated book really helped bring some of the images that he discussed to life. For me, the pictures made the difference in enjoying, rather than struggling to finish, the book. Finally, Fletcher's use of British terms such as hind and hart (for female and male red deer) is confusing and takes a little adjusting to. I actually had to Google "hind" (and other terms) to understand what he was referring to.

Fletcher did attempt to make up the Old World bias by devoting an entire chapter to North America deer. However, the one issue I had with that chapter and with the rest of the book in general, was that the book was overwhelmingly about human utilization of deer and less on deer biology and ecology. The author mentioned numerous times about hunting being a very necessary thing in today's world and sort of belittled the "urban population" that is against such things – little mention was made of society's evolving relationship with nature from utilization and romance to coexisting with and aesthetically enjoying wildlife among us. While I certainly agree that deer can become overabundant and human hunting is a necessary tool in certain instances, I felt that the book was too preachy on that topic. His quote on page 182 was probably accurate but sounded much like state wildlife departments here in North America, "As human urbanization and commuting become the norm, deer numbers grow (due to lack of hunters) and the image of deer as rare and precious mystical creatures risks being gradually displaced by perceptions of deer as suburban nuisances." Why not recognize that many people enjoy seeing them on a daily basis and that it enriches our lives even if they can pose a hazard to us? That isn't to say that deer hunting is not a major influence of societies from historical to present times, but it would have been refreshing to not view deer only as a game animal and commodity.

Fletcher had many chances to draw attention to other aspects of the Cervid family. For instance, there was essentially no discussion of predators. In fact, carnivores were mentioned a mere eight times in the book with most being in reference to wolves. Yet all of these were in passing and did not describe the importance of predators to both the evolution and management of deer species. It is well noted that even though humans have relied on deer over the course of our species' relative short existence, predators and prey have co-evolved with each other over a much longer period of time and the reason we see the fleetness of white-tailed deer, the robustness of bison and moose, and the regalness of wapiti is in part due to evolving defenses from predators such as wolves. I found it wrong that there would be no chapter devoted to the need to restore predators to landscapes where deer numbers are rising due to declines in human hunting. As the book currently stands, I think a better title would have been "Of Deer and Men", to steal the adage from Barry Lopez's famous 1978 book on wolves. To my point, at the end of the book Fletcher lists some associates and websites and all are related to deer farms and venison partnerships (i.e., to be used as food); no sources were given on deer ecology and biology.

Deer is an interesting and well written book that details the symbolism and the close association that humans and deer have had over centuries. Anywhere that people have lived, humans have made use of some of the 40 species of deer found worldwide. There are definitely things in this book that everyone will learn for the first time and that alone makes the book worthy of reading. And there are also many wonderful images that really bring the chapters to life. As long as one accepts the Old World (European) bias of the author, and the relative lack of description of deer biology versus the focus on deer folklore, symbolism, and human utilization of deer, this will be an enjoyable book to read.

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Dolphin

By Alan Rauch. 2014. The University of Chicago Press, 1427 East 60th Street, Chicago, IL, USA, 60637. 207 pages, 16.02 USD, Paper.

As Book Review Editor I receive unsolicited books. If I think the subject is specialised and I know an expert who writes well, I will ask them to review the book. Otherwise I send a notice to the 50 or so reviewers I have on file. About half of these people are regular reviewers, working on a book or more per year. Occasionally no one wants to volunteer, so, if I think I have sufficient knowledge, I will review it myself.

It has been my privilege to encounter dolphins on many occasions, most recently the Gangetic Dolphin in

the Koshi river of Nepal and the Pink and Grey River Dolphins in the Amazon. Therefore when this book sat unclaimed for two weeks I decided to review it myself. Before I got to the end of the first page I was entranced.

This little book has only six chapters, covering zoology, species, mythology, behaviour, dangers and as culture icons. In addition to the usual references (including websites) there is a two-page time-line from 1349 to present, showing our human interaction with this mammal.

The zoology chapter covers the fundamental biology of current dolphins. It summarises the evolution of these marine mammals from their deer-like ancestors over about 50 million years. The author follows their change from a four-legged and nose bearing animal to the flippered and blow-hole bearing mammal we know today. He covers the often weird ideas of early naturalists and the fish-mammal confusion. Rauch describes the adaptations that dolphins have made to live underwater – in their shape, vision and the internal body changes.

The chapter on species covers only enough dolphins to establish their diversity. From the whale-sized Orca to the 1.4 m Hector's dolphin and the more oddball river dolphins, the author describes those species that establish the boundaries of dolphin appearance.

Mythology discusses the real or fanciful stories that have arisen about dolphins. These range from dolphins with saw backs that slice open crocodile bellies, to the origin of "le Dauphin" of France and the numerous tales of dolphins rescuing humans. The story of Pelorus Jack, a Risso's Dolphin, has an intriguing twist, taking it from real to myth.

The chapter on Intelligence, Social Behaviour and Echolocation gives us an insight into the dolphin's world. It also tells how little we really know. In particular the author explains their wonderful ability to use echolocation. He also spends time recounting their "intelligence" although it seems futile to measure a marine mammal's brain power using human, land-based, thinking.

Apart from the natural dangers that dolphins face, we humans add other risks. A very small portion of humans directly kill dolphins for food. More frequently they die enmeshed in fishing nets set for tuna. Even those that get released from these nets are so injured that they die later. Pollution adds to their stresses. As an apex predator their fat contains pesticides, fire retardants and other carcinogens. They have been captured for zoos, research and even the military.

Dolphins have been intertwined with human culture for millennia. Our perspective has ranged from ferocious killers to children's soul mates. We have glorified them as surrogate humans and eaten them as fish. There are dolphin mascots, dolphin door handles, dolphin helmets and an amazing array of dolphin decorative art. We have kept dolphins as "pets" and performers. Yet none of this equates to seeing dolphins in the wild, behaving as dolphins should.

The author explores the role of dolphins in the media, from movies to comic books. He is not complimentary of the way we have portrayed these mammals. We tend to glorify these animals as smart, semi-humans while ignoring their real and fascinating lives.

I enjoyed reading all the chapters and felt the author presented information in an unbiased manner that was thought provoking. Dolphins is a fascinating and well written book and I am delighted that I was forced to "volunteer."

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Wild Again: The Struggle to Save the Black-footed Ferret

By David Jachowski. 2014. University of California Press, 155 Grand Avenue, Suite 400, Oakland, CA, USA, 94612–3758. 256 pages, 34.95 USD, Cloth.

As I read author David Jachowski's book, *Wild Again*, I envisioned a time when the Great Plains were undisturbed by human activity and all wildlife existed in their historical pre-European abundance, including black-footed ferrets and their prairie dog prey. This would be a time before diseases, such as plague and distemper, ravaged species that had not co-evolved with those ailments. Instead, my vision included large areas, many thousands of acres, of prairie dog colonies that had grazing animals, such as pronghorn and bison, on it and predators, like wolves and grizzly bears, following them.

Jachowski offers an engaging, personal account of his involvement in black-footed ferret (*Mustela nigripes*) recovery efforts. Once feared extinct, rediscovered in Meeteetse, WY in 1981 (page 31-35), and still one of North America's rarest mammals, this small weasel exemplifies the ecological, social, and political challenges of conservation in the West, including the risks involved with intensive captive breeding and reintroduction to natural habitats. As the jacket cover of the book indicates, the author draws on more than a decade of experience working to save the ferret to base his writings, and his unique perspective and informative anecdotes reveal the scientific and human aspects of conservation as well as the immense dedication required to protect a species on the edge of extinction. By telling one story of conservation biology in practice —its routine work, triumphs, challenges, and inevitable conflicts—*Wild Again* gives readers a greater understanding of the conservation ethic that emerged on the Great Plains as part of one of the most remarkable re-

covery efforts in the history of the Endangered Species Act. I couldn't agree anymore with that accurate statement and essential summary of the volume.

I greatly appreciated the personal focus of *Wild Again* which the author unabashingly states both in the jacket cover as well as in the *Prologue* section. Jachowski comments that the book is written for everyone and is not intended to be a comprehensive, technical review of ferrets (page vii), yet the 18 page *Further Readings* chapter at the end makes it very authoritative and comprehensive, in my opinion. One gets to learn of the highs and lows of being a field biologist and many of the author's experiences could be substituted for any animal, such as little funding, political influence and interference, difficult living situations, and self-sacrifice beyond most jobs. In my research on eastern coyotes/coywolves, I have often been criticized for being too personal and liking my study subjects, so it was very refreshing to read the commentary on conservation biology being a blend of advocacy and science (page 29). May be our politicians, including within wildlife agencies, will one day better appreciate that scientists are people too and should be able to offer their professional as well as personal opinions without fear of repercussions on their job and career security.

I was amazed that an author around my age (mid to late 30s) could have such of a developed and eloquent writing style, in addition to a well balanced perspective, as he wove many diverse accounts from personal to professional stories into one wonderful, easy-to-read adventure. For example, his beginnings as a child helping researchers at his father's Patuxent field research station, his late-night bar episodes, and his personal relationship issues of living on the Great Plans in isolation are captivating and mentioned throughout numerous sections of the text. And the descriptions of spotlighting ferrets at night, mapping prairie dog burrows during the day, detailing nuances of ferret behaviour (such as females testing males during coitus, page 97), trying to captive breed and increase ferret numbers, and conducting research in many different regions, from Montana to Mexico, made the over 200 page hardcover a real page turner. This is saying something considering that book sales and traditional book reading for my generation (and in general) are on the decline as the internet and information age produces news items (e.g., global warning, poaching, habitat loss) that seemingly change every few minutes, and as Jachowski explains (page 210), this makes it difficult for even professional conservation biologists to figure out what to protect and how to react to such large volumes of details.

While readers may be turned off by the apparent negative tone and unfortunate outcomes that are often discussed in *Wild Again*, such as plague killing off prairie dog colonies and people poisoning prairie dogs right at the edge of ferret recovery areas, I strongly believe that these occurrences must be documented and included as these are the personal and professional experiences of many wildlife biologists the world over. There certainly aren't always positive endings in the world of wildlife research as evidenced by the fact that even after 22 years (1991-2013) and releasing more than 3,000 captive reared ferrets at 19 reintroduction areas, the black-footed ferret is only about a quarter of the way to being numerically recovered (page 212), which involves at least 30 self-sustaining adults inhabiting 10 different locations. Given that the main prey of ferrets, prairie dogs, are candidates for Endangered Species Act listing, it is not surprising that they still face a long and uphill climb, even with advocates like Jachowski trying to help them along.

The author (page 211) nicely concludes with a discussion of the direct, utilitarian benefits to humankind from conserving biodiversity, such as food, medicine, and water quality, yet he argues that sentimentality is another reason why we preserve nature and animals like ferrets and the prairie dogs that they depend on. Jachowski stresses that it is perhaps our most selfless act to try to preserve something when it is not in the strictest sense physically, energetically, or evolutionary beneficially to do so (page 211). Even though it is the law in the US to protect endangered species, I also believe that defending and helping to preserve a controversial animal is courageous given the usual hatred, prejudice and paranoia displayed to many endangered or politically challenging animals (see page 175-177). While I was shocked to learn that prairie dog poisoning is still allowed and practised in the US, and find it pathetic that this is a publically funded activity to this day, I found it entirely predictable that entrenched (and I would argue hypocritical) politicians will fight on the behalf of ranchers and farmers to continue such expensive, environmental destructive, and indefensible activities. In fact, Jachowski explained (page 175) that in South Dakota, hatred of prairie dogs still divides the community as easily as religion or politics does in other parts of the country.

The manuscript has only a few, minor grammatical errors, and most descriptions seem accurate and realistic for the locations discussed. There are pictures dispersed throughout the book which adds character and enables the reader to see prairie dogs, black-footed ferrets, and some of the locations where the author conducted research. However, not knowing the area that well, and doing what the author says most people do (i.e., flying over the plains from the forests [of suburbia] where I live to the mountains of places like Yellowstone Park where I vacation), I wish there were more maps to see the different places that the author visited and studied ferrets in (there is a map on page 158 but it is of four territories of female ferrets in his SD study area). Other than the lack of maps, my only other inconsequential complaint was really just three further questions that were not answered in the text but which I pondered: (1) Because the book was so comprehensive, personal, and well articulated, I wanted to know why Jachowski was no longer with the ferret team. I did find it entirely predictable for him to publish his findings after his decade plus stint studying ferrets, as expressing his views while still employed would

have likely (and most unfortunately) predisposed him to ridicule and possible even job firing as he described occurring for other people advocating for ferrets (e.g., page 160). (2) What about his wife mentioned in the acknowledgments (page 216)? He discussed other relationships he had, and how he chose the grasslands over the woman he loved (page 5), so how did he meet her? And (3), how was he able to move around so much during his job, such as to the Conata Basin of South Dakota from the UL bend in Montana. And why did he have to pay out of pocket for things, such as housing in SD, if he was working for the federal government? I wonder if he worked a part-time (seasonal) job with the federal government, known as a 1039 term position where one cannot work more than 6 months in a year, and then volunteered the rest of the time. These three questions would have really rounded out the book, which essentially covered from his childhood to the present (2013, I believe).

As you can probably tell, if I am critical of such trivial details that means I really was enthralled with *Wild Again* and was able to comprehend every major section and storyline that happened within. I recommend it for anyone who is interested in wildlife, species recovery, and stories and adventures of this highly endangered and endemic North American predator, the black-footed ferret. It is a delightful read and well worth the time and money to learn about this little known and studied predator, and the grassland ecosystems and prairie dogs that it relies upon.

JONATHAN WAY

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OTHER

Ecology

By Michael L. Cain, William D. Bowman, and Sally D. Hacker. 2014. 3rd Edition. Sinauer Associates, Inc., Publishers, Sunderland, MA, USA, 01375-0407. 596 pages, 134.95 USD, Cloth.

The third edition to an already useful text contains some very important changes and improvements from the two earlier editions. The author's goal for this edition was to improve the usefulness of the text for both students and instructors and as with previous editions the focus in the undergraduate student. Aside from the text being updated, I will highlight the significant changes as well as provide a general overview of the text.

Ecology is composed of 25 chapters arranged into 7 Units to cover the complete depth of the field of ecology. The Units represent the scale and scope of ecology; individual, population, community, ecosystem, and global. In addition, there are units on the major ecological interactions of competition, predation, parasitism, and mutualism/commensalism, and evolutionary ecology. Natural selection forms the overlying basis for the entire text.

The content of this edition includes a new chapter on behavioural ecology which brings into focus the importance that behavior plays in populations and the structure of communities as well as interactions. It includes not only the ways that organisms live in aggregations but also foraging and mating behavior with the context always focused on the evolution of the behaviour as an important life history strategy to enhance fitness.

Several important features are worthy of note. First of all, the authors have included exercises that require analyzing data. This is not only an essential skill in ecology but also aids in developing critical thinking skills. The authors have continued to provide case studies of important concepts but have also added "Connections in Nature" which shows how chapter concepts relate to the concepts in other chapters.

Pertinent to one of our greatest ecological challenges, this edition has a web feature "Climate Change Connections" which provides some useful material to relate ecological concepts to issues surrounding climate change. Most chapters have of this edition have examples relating to climate change.

An example of another new feature are the "Ecological Toolkit" boxes. These boxes highlight important techniques used by ecologists. Among the interesting ones are stable isotope analysis and estimation of population abundance and population growth rates.

The supplemental online content appears to be of high quality but at the time of review (05/2014) the publisher only has material for one chapter (4) available for examination. There appears no indication that this content will require a subscription although certainly this could change once the site is completed.

This edition has many other features that make it an improvement to an already good text. I would strongly recommend using this text if you are not already using the second edition and if you are, I recommend upgrading to this edition. If you want a personal text that can be used to facilitate self-learning of ecology or updating your ecological knowledge, this text is recommended. I can also recommend this edition as a reference if you wish to have an ecology text on your shelf. The addition of online content, especially if it remains free as noted above, enhances the value.

ROGER D. APPLEGATE

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The Once and Future Great Lakes Country: An Ecological History

By John L. Riley. 2013. McGill-Queen's University Press, 1010 Sherbrooke West, Suite 1720, Montreal, QC, Canada, H3A 2R7. 516 pages, 39.95 CAD, Cloth.

Wow. Check out this book if you are craving a read with vast dimensions. I don't mean the physical book, either. That, in hardcover, has a comfortably satisfying heft like your favourite dictionary or rock purloined from nature. The cover alone is breathtaking, an oblique aerial view of a landscape in orange and gorgeous water blue. The book doesn't identify the place, and I couldn't either. Even if it is cover art, to provide an aerial photo with no label is the perfect way to torture a geographer, or at least to cause one to spend a lot of time scanning around on Google Earth. Instead I enlisted friends to the case via Facebook. We think, thanks to Sean Blaney and Becky Whittam, that it's Matchedash Bay looking north to Georgian Bay.

I will declare my bias. I know many reading this join me in calling the Great Lakes country home, our lives framed by these lakes. The Bruce Peninsula and Lake Huron shoreline, for instance, have scoured our childhood memories. The Waterloo region was the landscape and ecology lab through university. Then we were in thrall to the thrum of bird migration over the Lake Erie shore. Ian Tamblyn's *Woodsmoke and Oranges* embodies our time with Lake Superior. John Riley's work is rich in time, drilling into prehistory and telescoping into the future. We can place it on the same library shelf as other ecological and environmental histories, both regional and broader in scope, but if offers quite a bit of cultural introspection too, an element you might not always find elsewhere.

At the time of publication, Riley was a senior science advisor for the Nature Conservancy of Canada. He begins this story on his own land where with his family he occupies an old farm (there are thousands like it, he says) in the Great Lakes basin. From there he builds outward in both time and geography to follow this remarkable region through so many passages. It is very well-written. It pulled me along, with loads of fascinating information, analysis and evocation of landscapes, wildlife, people and peoples. Human beings are the significant force of ecological change for much of the book's span, so their history and influence are sensitively portrayed. Riley skillfully stitches past with present and future so that the reader never forgets the relevance of any one to the other. The book also is thoroughly referenced and noted, with much reliance on first person accounts and other authors.

Just to whet your curiosity, I offer these chapter titles: "Land Beyond Memory: Before 1500"; "Wilding the Land with War: the 1700s"; "Taming the Unforested: Prairies, Alvars, Barrens, Cliffs, Bogs and Fens" and "Restoration: A New Native Landscape". I am a fool for prehistory and early history, so those chapters held me more tightly than the later ones. The final chapters contain large amounts of optimism, making the case that the current trend is actually toward conservation rather than the opposite. The optimism puzzles me, but I will take it because I so thirstily want it.

I can recommend this book without reservation. You may or may not take issue with the author's points of view on some subjects, or interpretation of historical records (there is a heck of a lot to consider!) but it is finely presented for your inspection. As well, Riley's writing voice is utterly human and companionable. The hardcover edition is lovely to have. I bought the e-book as well, for ease of searching by word.

BEV MCBRIDE

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NEW TITLES

Prepared by Roy John

† Available for review * Assigned
Currency Codes – CAD Canadian Dollars, USD U.S. Dollars, EUR Euros, AUD Australian Dollars.

ZOOLOGY

A Checklist of North American Amphibians and Reptiles: The United States and Canada. Volume 1 – Amphibians. By M. J. Fouquette, Jr., and Alan Dubois. 2014. Xlibris LLC, 1663 Liberty Drive, Suite 200, Bloomington, IN, USA, 47403. 613 pages, 34.95 USD, Cloth, 29.95 USD, Paper. (Request for a review copy refused by publisher.)

* **Animals of the Serengeti.** By Adam S. Kennedy, and Vicki Kennedy. 2012. Princeton University Press, 41 William Street, Princeton, NJ, USA, 08540-5237. 152 pages, 27.95 USD, Paper.

Beetles of Eastern North America. By Arthur V. Evans. 2014. Princeton University Press, 41 William Street, Princeton, NJ, USA, 08540-5237. 560 pages, 35.00 USD, Paper.

* **Birds of the Kenya's Rift Valley.** By Adam S. Kennedy. 2014. Princeton University Press, 41 William Street, Princeton, NJ, USA, 08540-5237. 264 pages, 29.95 USD, Paper.

* **Birds of the Serengeti.** By Adam S. Kennedy. 2012. Princeton University Press, 41 William Street, Princeton, NJ, USA, 08540-5237. 176 pages, 27.95 USD, Paper.

The Thing with Feathers: The Surprising Lives of Birds and What They Reveal About Being Human. By Noah Strycker. 2014. Penguin Group (USA), 375 Hudson Street, New York, NY, USA, 10014-3657. 304 pages, 18.37 USD, Cloth.

The Sibley Guide to Birds, Second Edition. By David Sibley. 2014. The Knopf Doubleday Group, 1745 Broadway, New Yörk, NY, USA, 1001. 624 pages, 40.00 USD, Cloth.

The ROM Field Guide to Butterflies of Ontario. By Peter Hall, Colin Jones, Antonia Guidotti, and Hubley Brad. 2014. Royal Ontario Museum, 100 Queen's Park, Toronto, ON, Canada, M5S 2C6. 64 pages, 29.99 CAD, Cloth.

* **Wild Again - The Struggle to Save the Black-Footed Ferret.** By David S. Jachowski. 2014. University of California Press, 2120 Berkeley Way, Berkeley, CA, USA, 94704-1012. 256 pages, 34.95 USD, Cloth.

How Snakes Work: Structure, Function and Behavior of the World's Snakes. By Harvey B. Lillywhite. 2014. Oxford University Press, North Kettering Business Park, Hipwell Road, Kettering, Northamptonshire, UK, N14 1UA. 224 pages, 35.00 GBP, Cloth.

* **Wildlife of the Caribbean.** By Herbert A. Raffaele, and James W. Wiley. 2014. Princeton University Press, 41 William Street, Princeton, NJ, USA, 08540-5237. 304 pages, 19.95 USD, Paper.

OTHER

***Amphibian Conservation - Global Evidence for the Effects of Interventions.** By Rebecca K. Smith, and William J. Sutherland. 2014. Pelagic Publishing, P.O. Box 725, Exeter, UK, EX1 9QU. 279 pages, 29.99 GBP, Paper.

Experimental Evolution and the Nature of Biodiversity. By Rees Kassen. 2014. Roberts and Company, 4950 S. Yosemite Street, F2 #197, Greenwood Village, CO, USA, 80111. 288 pages, 45.00 USD, Cloth.

The Analysis of Biological Data. By Michael Whitlock, and Dolph Schluter. 2014. Roberts and Company, 4950 S. Yosemite Street, F2 #197, Greenwood Village, CO, USA, 80111. 704 pages, 123.75 USD, Cloth.

Ecology – Third edition. By Michael L. Cain, William D. Bowman, and Sally D. Hacker. 2014. Sinauer Associates, Inc., 23 Plumtree Road, P.O. Box 407, Sunderland, MA, USA, 01375-0407. 648 pages, 129.95 USD, Cloth.

Whale-watching: Sustainable Tourism and Ecological Management. By James Higham, Lars Bejder, and Rob Williams. 2014. Cambridge University Press, University Printing House, Shaftesbury Road, Cambridge, UK, CB2 8BS. 110.00 CAD, Cloth.

News and Comment

Upcoming Meetings and Workshops

International Society for Behavioral Ecology (ISBE) Conference 2014

The 15th International Behavioral Ecology Congress to be held 31 July – 1 August 2014 by Hunter College of the City University of New York (CUNY) and the behavioral ecology research community based at various CUNY campuses and New York University. Registration is currently open. More information is available at http://www.isbe2014.com.

Conservation and Biology of Tortoises and Freshwater Turtles Annual Symposium

The 12th annual symposium on the Conservation and Biology of Tortoises and Freshwater Turtles to be held 4–7 August 2014 in Orlando, Florida. The meeting, sponsored by Zoo Med Laboratories, Inc., is co-hosted by the Turtle Survival Alliance and the IUCN Tortoise and Freshwater Turtle Specialist Group (TFTSG). The meeting represents the largest gathering of non-marine turtle biologists in the world and provides an unmatched opportunity for networking and strategizing turtle conservation. More information is available at http://www.turtlesurvival.org/get-involved/con ference#.U16FgldB870.

Ecological Society of America Meeting 2014

The 99th annual meeting of the Ecological Society of America to be held 10–15 August 2014 at the Sacramento Convention Center in Sacramento, California. The theme of the meeting is "From Oceans to Mountains: It's All Ecology" and registration is currently open. More information is available at http://esa.org /am/.

Northeast Partners in Amphibian and Reptile Conservation Meeting 2014

The 15th annual meeting of the Northeast Partners in Amphibian and Reptile Conservation (NEPARC) to be held 13–15 August 2014 Allegany State Park, Salamanca, NY. NEPARC is an active, diverse, and inclusive partnership dedicated to the conservation of amphibians and reptiles and their habitats throughout northeastern North America. Poster abstract deadline is 11 July 2014. More information is available at http:// www.northeast parc.org/meetings/index.htm.

International Ornithological Congress 2014

The 26th International Ornithological Congress (IOC) to be held 18-24 August 2014 at Rykkio University in Tokyo, Japan. More information is available at http:// Ioc26.jp.

American Ornithologists' Union/Cooper Ornithological Society/Society of Canadian Ornithologist Meeting 2014

Annual meeting of the American Ornithologists' Union (132nd Stated Meeting), the Cooper Ornithological Society (84th Stated Meeting), and the Society of Canadian Ornithologists (32nd Stated Meeting) to be held 23–27 September 2014 at the YMCA of the Rockies in Estes Park, CO. The meeting will feature 5 days of workshops, contributed scientific papers, posters, and invited speakers, including symposia that look at exciting new approaches and results in ornithology. More information is available at https://www.bird-meetings.org/aoucossco2014/default.asp.

Raptor Research Foundation Conference 2014

Raptor Research Foundation 2014 Conference to be held 24-28 September 2014 at the Emerald Beach Hotel in Corpus Christi, Texas. Co-Hosts are the Caesar Kleberg Wildlife Research Institute at Texas A&M University, Kingsville and HawkWatch International. More information is available at http:// www.raptor-researchfoundation.org/conferences/cur rent-conference.

Raptor Workshop: *Introduction to Raptor Field Techniques*

Raptor Services, LLC presents 5-day workshops to be held in Stevens Point, Wisconsin by Gene Jacobs of the Linwood Springs Research Station. This introductory level field course is designed to instruct students in a full-range of field techniques used in the study of raptors. The workshop is offered every June with an emphasis on learning breeding season field techniques and again in August, September, and October, with an emphasis on migration and winter research techniques. Receive first-hand experience working with: live raptors, capturing, handling, banding techniques, broadcast call surveys, tree climbing, rappelling, blood sampling and more. Summer Sessions: 2–6 June and 23– 27 June; Fall sessions: 25–29 August and 13–17 October 2013, and two weekend sessions 5,6,7,13,14, September. Cost is $450 and space is limited (6–8 students per workshop). More information is available at http://www.raptorresearch.com /workshop.htm.

Retirement of Associate Editor C. D. Bird

After serving *The Canadian Field-Naturalist* as Associate Editor for almost 40 years, longer than any of his contemporaries except for ornithologist Tony Erskine, Dr. Charles Durham Bird has stepped down in early 2014. He primarily reviewed botanical submissions but also some in entomology and general natural history. First appointed in 1975 when Lorraine Smith was journal editor, he has continued without interruption through the subsequent editorial terms of Francis Cook and Carolyn Callaghan. In recognition of his contributions he was made an Honorary Member of The Ottawa Field-Naturalists' Club in 2005 (see *Canadian Field-Naturalist* 119(4): 614), and has received numerous Alberta awards for his contributions. Charley was born in 1932, a son of Ralph Durham Bird (1901–1972, *see* tribute in 1972 *Canadian Field-Naturalist* 86(4): 393–399). The senior Bird was a prairie entomologist with Agriculture Canada, widely known for his classic monograph *Ecology of the Aspen Parkland*, (1961).

Although born in Oklahoma when his father was teaching at The University of Oklahoma, Charley was raised in Manitoba, where he developed early interests in botany from his mother (Lois Gould, 1905–1959), and entomology from his father. He obtained a BSc from University of Manitoba in 1956, MSc from Oklahoma University, Stillwater, in 1958, and PhD from Oklahoma State University in 1960. His thesis for the latter was on vegetational and waterfowl changes in P.F.R.A. reservoirs in west-central Canada based on surveys for Canadian Wildlife Service in the summers of 1956-1959. In 1960-1962 he held a National Research Council Postdoctoral Fellowship at the University of Alberta, became an Assistant Professor of Botany in 1962, Associate Professor in 1967, and Full Professor in 1974. He and his wife Ann purchased a farm near Mirror, Alberta, in 1975 and he took early retirement from the university in 1979. In 1992 they sold the farm and retired in Erskine, Alberta.

He has contributed over 300 articles, notes, book reviews, and reports, notes in print and electronic media, primarily on mosses, lichens, liverworts and Lepidoptera but also including tributes, conservation, and extended family history items. He has collected over 37,000 insects for eventual deposit in collections of the University of Alberta and 36,000 plants largely already deposited there or in various other herbaria. Presently, Charley is continuing his work on the Lepidoptera of natural areas in south-central Alberta as well as his research on family genealogy. In addition, he is conducting inventory work of the biota of the J.J. Collett Natural Area and contributing regularly to their website. Like Tony Erskine, he has agreed to review occasional future papers submitted to *The Canadian Field-Naturalist* whenever his expertise and perspective are particularly needed.

FRANCIS R. COOK

Obituary – Farley Mowat 1921–2014

An ardent, outspoken conservationist, fervent Canadian, and world acknowledged northern literary success, Farley Mowat, has died at his home at Port Hope, Ontario, 8 April 2014. He is survived by his wife Claire.

Mowat showed an affinity for natural history, writing, and controversy early (see Cook 2003), starting as a teenager with a bird column in the *Saskatoon Star-Phoenix* in the mid 1930s as he recounted in *Born Naked* (1993). After some initial success, this was terminated when he submitted an enthusiastic account of the sexual activities of some of his subjects that was considered too lurid for newspaper public of the time.

Mowat seemed destined to a career as a scientist when he went to the University of Toronto and took his first collecting expedition with fellow zoology students Frank Banfield and H. Hord to Saskatchewan in the summer of 1939 (as recalled in *Otherwise*, 2008). Banfield covered mammals and Mowat and Hord birds, and sold their collections to the Royal Ontario Museum to finance the trip. Both Mowat and Banfield subsequently enlisted in Canadian army and served overseas in World War II but wrote up their field results and published in *The Canadian Field-Naturalist*. Characteristically, Banfield submitted his account before going overseas and Mowat only after his return.

The latter was apparently the first and last formal scientific paper Mowat wrote, but far from his last expedition or literary publication. After the war he was field assistant in the Northwest Territories to the legendary and irascible North American mammalogist and naturalist, Francis Harper. A clash of personalities soon led Farley to undertake his own explorations separately (Harper later extracted a reciprocal promise that neither would mention the other in their respective future writing, a promise also extracted from Mowat by later field companions for their lifetimes).

A research proposal led to his hiring by the Canadian Wildlife Service for the four-researcher Caribou survey which Banfield headed. Later, however, Banfield was ordered to fire Mowat by the chief of the Wildlife Service due to local complaints and lack of advance formal approval for some activities.

Cut loose, Mowat turned to writing – notably *People of the Deer* (1952) *and Never Cry Wolf* (1963), on Mowat's conclusions on the plight of some native northern people and on the life and human persecution of wolves, respectively. Although early reviewers of both were captivated by the writing style and subjects, later in depth reviews by researchers familiar with areas, animals, and people, were generally hash due to frequent wanderings from fact in both. Pre-eminent among the critics were the prominent botanist Erling Porsild (see Duthan 2012) and mammalogist Frank Banfield (see Morris 1990) whose reviews appeared in 1952 (*The Beaver* June: 47) and 1964 (*The Canadian Field-Naturalist* 78: 52-54), respectively. The reaction to the former is extensively covered by Dathan 1997: 569–594; the latter drew a response to the CFN Editor, reportedly from the wolf "Uncle Albert", defending Mowat's account (*The Canadian Field-Naturalist 78: 206*).

Urged on initially by the resourceful promoter and publisher of Canadian writers, Jack McCelland (see King 1998), Mowat produced over 40 books which were widely translated worldwide with sales of more than fourteen million copies on topics ranging from his experiences in WWII (particularly in *And No Birds Sing* 1979 – perhaps his finest writing), pets, boats, whales, overharvest of ocean resources (*Sea of Slaughter* 1984), a biography of Dian Fossey (1987), and serial portions of autobiography.

Mowat never finished his degree and was lost to formal science but his writings gained and entertained a huge audience of readers as he was above all else a really good story-teller with an appealing message. Although he often admitted a tendency not to let the facts get in the way of a good story, his writings made an impact by focusing on basic truths as he saw them and his delight in goring beaurocracy. By adding to a growing public focus on wildlife and conservation they helped promote pressure for increased governmental protection at all levels and influenced young scientists to research careers on the problems faced by the creatures with which we share the earth. His appreciation of northern fauna and his defense of wolves gained a large appreciative audience far beyond North America particularly in the country which also has vast arctic and boreal areas, the Soviet Union, which he later also was invited to visit, thus providing material for some subsequent books.

See also:

Banfield, Frank A. 1942. Notes on Saskatchewan mammals. Canadian Field-Naturalist 55(8): 117–123.

Cook, F. R. 2003. [Book review] Farley: The Life of Farley Mowat *By* James King. Canadian Field-Naturalist 117(3): 509–510;

Dathan, Wendy. 2012. The Reindeer Biologist: Alf Erling Porsild, 1901–1997. University of Calgary Press, Calgary, Alberta.

Morris, R. D. 1998. Obituary Alexander William Francis Banfield: 1918–1996. Journal of Mammalogy 79(1): 364–369.

Mowat, F. M. 1947. Notes on the birds of Emma Lake, Saskatchewan. Canadian Field-Naturalist 61(3): 105–115.

King, R. 1998. Jack: A Life with Writers. McCelland and Stewart, Toronto, Ontario.

FRANCIS R. COOK

Editor's Report for Volume 127 (2013)

Mailing dates for issues in volume 127:
(1) 15 July 2013
(2) 21 October 2013
(3) 4 December 2013
(4) 14 January 2014

In an effort to get caught up in the production schedule, we published 8 issues of *The Canadian Field-Naturalist* over a period of 14.5 months (3 October 2012 – 14 January 2014). Not surprisingly, submission rates have increased concomitantly over the past few years; a 56% increase since 2011. To ensure that we will keep up with the higher number of submissions, we have increased our team of Associate Editors.

The Canadian Field-Naturalist remains an important forum for dispersing science on the distribution, taxonomy, biology, behaviour, ecology, and conservation of species across a broad range of taxa in North America. In volume 127, several new records were published of species of mammals, fish, birds, insects, lichen, plants, plesiosaurian, and ichthyosaur in particular regions of Canada and one new record for the country. Some of the other varied topics include the biology of rare, reintroduced, and invasive species, improved methods for detecting species at risk, impacts of road infrastructure and traffic on wildlife, effects of management actions on the conservation of rare habitats, interspecific interactions, species surveys in under-surveyed regions, and analyses of datasets spanning many decades. As some habitats and species undergo increased pressure from the effects of anthropogenic activity, the utility of CFN to conservation will increase via the provision of scientific information based on field studies. The values that led to the creation of CFN in the 1800s continue to be relevant today.

Trina Rytwinski, Assistant Editor, edited content, acted as an occasional Associate Editor, and acted as Editor-in-Chief for two months. Elizabeth Morton proofed and edited manuscripts; Wendy Cotie typeset galleys, provided corrections for page proofs, and created pdfs; Roy John, Book Review Editor, requested books for review, selected reviewers, edited submitted reviews, and prepared the new titles listings; Jay Fitzsimmons, Journal Manager, managed financial accounts, issue mailing, and requests for back issues, conducted journal promotion through Twitter and other means, and provided digital content to subscribers. William Halliday prepared the Index with proofreading by Trina Rytwinski and Dan Brunton. Sandra Garland, webmaster of the Ottawa Field-Naturalists' Club, posted tables of contents, abstracts, and pdfs on the CFN section of the OFNC website. Our Associate Editors managed manuscripts, provided reviews and recommendations, and guided authors through the revisions process. The Publication Committee, chaired by Dan Brunton and consisting Paul Catling, Jay Fitzsimmons, Sandra Garland, Tony Gaston, Karen McLachlan-Hamilton, Frank Pope, and Jeff Saarela effectively guided the operation of the journal. We are indebted to our very dedicated and effective team.

A summary of the distribution of memberships in the Ottawa Field-Naturalists' Club and subscribers to *The Canadian Field-Naturalist* for 2013 is provided in Table 1. The number of articles and notes in Volume 127 is summarized in Table 2 by topic; totals for book reviews and new titles is given in Table 3; and the distribution of content by page totals per issue is provided in Table 4. Manuscripts (excluding book reviews, notices and reports) submitted to *The Canadian Field-Naturalist* totalled 84 in 2013. Of these, 73 were accepted for publication, and 30 were published in volume 127, along with 16 manuscripts submitted in 2012 and revised in 2013. A total of 25 Articles, 18 Notes, 3 Tributes, and 3 Essays were published in 2013.

The following Associate Editors managed, assessed and reviewed manuscripts published in volume 127 (number of manuscripts in parentheses): R. Anderson, Canadian Museum of Nature, Ottawa ON (4); C. Callaghan, Luskville QC (3); P. M. Catling, Agriculture and Agri-Food Canada, Ottawa ON (3); F. R. Cook, Emeritus Research Associate, Canadian Museum of Nature, Ottawa ON (5); J. Foote, Algoma University, Sault Ste. Marie ON (4); S. Jung, Yukon Government, White-

TABLE 1. The 2013 circulation of The Canadian Field-Naturalist (2012 in parentheses). Compiled by Jay Fitzsimmons from mailing list for 127(4).

Subscriber Type	Canada		USA		Other		Total	
Memberships								
Family & Individual	89	(89)	8	(8)	1	(1)	98	(98)
Subscriptions								
Individual	79	(81)	28	(30)	3	(3)	110	(114)
Institutional	127	(122)	159	(164)	28	(27)	313	(314)
Total	295	(292)	195	(202)	32	(31)	522	(525)

TABLE 2. Number of research and observation articles and notes published in *The Canadian Field-Naturalist*, Volume 127, by major field of study.

Subject	Articles	Notes	Total
Mammals	7	7	14
Birds	6	5	11
Amphibians and Reptiles	1	1	2
Fish	2	1	3
Plants	3	2	5
Insects	2	2	4
Other	4	0	4
Total	25	18	43

TABLE 3. Number of reviews and new titles published in the Book Review section of *The Canadian Field-Naturalist*, Volume 127, by topic.

	Reviews	New Titles
Zoology	23	47
Botany	3	4
Environment	4	2
Miscellaneous	7	28
Children	1	0
Total	38	81

TABLE 4. Number of pages per section published in *The Canadian Field-Naturalist*, Volume 127 (2013), by issue.

	Issue				
	1	2	3	4	Total
Editorials	0	0	1	0	1
Articles	56	72	59	29	217
Notes	19	14	12	20	65
Book Reviews*	15	9	10	12	46
News and Comment, Reports**	6	5	18	7	34
Tributes	6	0	0	14	20
Index				10	10
Total	102	100	100	92	394

*Includes reviews and new titles listings
**Includes CFN Editor's report, Minutes of the OFNC Annual Business Meeting, and OFNC Awards report.

horse YT (3); D. F. McAlpine, New Brunswick Museum, St. John NB (5); D. W. Nagorsen, Mammalia Biological Consulting, Victoria BC (5); C. Renaud, Canadian Museum of Nature, Ottawa ON (3); T. Rytwinski, Carleton University, Ottawa ON (3); J. Saarela, Canadian Museum of Nature, Ottawa ON (7).

The following referees reviewed manuscripts published in volume 127 (number of manuscripts reviewed >1 in parentheses): Becky Abel, The Trumpeter Swan Society, Plymouth MN; Ken Abraham, Ontario Ministry of Natural Resources, Peterborough ON; Paul Abram, Carleton University, Ottawa ON; Jim Atkinson, University of Guelph, Guelph ON; Shannon Berch, BC Ministry of Environment, Victoria BC; Sean Blaney, Atlantic Conservation Data Centre, Sackville NB; Edward Bork, University of Alberta, Edmonton AB; Ernie Brodo, Canadian Museum of Nature, Gatineau QC; Ronald J. Brooks, University of Guelph (retired), Guelph ON; Dan Brunton, Ottawa ON; Angela Burkinshaw, Alberta Environment and Sustainable Resource Development, Red Deer AB; Naomi Cappuccino, Carleton University, Ottawa ON; Kevin Cash, Environment Canada, Ottawa ON; Dr. Stephen Clayden, New Brunswick Museum, Saint John NB; Philip A. Cochran, Saint Mary's University of Minnesota, Winona MN; Daniel Cristol, The College of William & Mary Williamsburg VA; Dr. Rick A. Cunjak, University of New Brunswick, Fredericton NB; Fredrik Dalerum, University of Pretoria, Pretoria South Africa; Margaret F. Docker, University of Manitoba, Winnipeg MB; Erica Dunn, scientist emeritus, Environment Canada, Ottawa ON; Tony Erskine, Sackville NB (2); Kris Everatt, University of Pretoria, Pretoria South Africa; Lenore Fahrig, Carleton University, Ottawa ON; Dianne Fahselt, University of Western Ontario, London ON; Jennfier Foote, Algoma University, Saulte Ste. Marie ON; Jan Freiwald, University of California, Santa Cruz CA; Marcel Gahbauer Stantec, Montreal QC; John A. Gilhen, Nova Scotia Museum of Natural History, Halifax NS; Steve Hager, Augustana College; Rock Island IL; Sarah Hambleton, Agriculture and Agri-Food Canada, Ottawa ON; Mark Hanson, Fisheries and Oceans Canada, Moncton NB; Lee Hastie, University of Aberdeen, Aberdeen Scotland; Mark Hipfner, Environment Canada, Delta BC; Howard M. Huynh, Texas Tech University, Lubbock TX; Lawrence Igl, U.S.G.S. Northern Prairie Wildlife Research Center, Jamestown ND; Danny Ingold, Muskingum University, New Concord OH; Todd Katzner, West Virginia University, Morgantown WV; Charles Krebs, Professor Emeritus, University of British Columbia, Vancouver BC (2); Karl Larsen, Thompson Rivers University, Kamloops BC; Cori Lausen, Wildlife Conservation Society Canada, Kaslo BC; Zoe Lindo, University of Western Ontario, London ON; Eric Lofroth, Victoria BC; Scott McBurney, Atlantic Veterinary College, University of Prince Edward Island, Charlottetown PEI; Dr. Nick McCann, Minnesota Zoo, Apple Valley MN; Dave Mech, University of Minnesota, St. Paul MN; Dr. David A. Methven, University of New Brunswick, Saint John NB; Randall Miller, New Brunswick Museum, St. John NB; James Miskelly, Royal BC Museum, Victoria BC; Ron Moen, University of Minnesota, Duluth MN; Eric Moise, University of Western Ontario, London ON; Anders Pape Moller, Université Paris-Sud, Orsay Cedex France; Ralph Morris, Brock University (retired), St. Catharines ON; Marion Munroe, Nova Scotia Provincial Museum, Halifax NS; Jan Murie (retired), University of Alberta, Edmonton AB; Dr. Clay Nielson, Southern Illinois University, Carbondale IL; Michael Oldham, Ontario Ministry of Natural Resources, Peter-

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The journal was printed at Gilmore Printers, Ottawa. Thanks to Gilmore for overseeing production and printing. I am grateful to President Fenja Brodo and Council of the Ottawa Field-Naturalists' Club for their support of the journal. I am also grateful to all of the individual subscribers and authors who encouraged our team as we strive to provide a high-quality scientific journal on natural history. A special thank you to Liz Morton for her years of service as copy editor, and to Leslie Cody for producing the Index. Finally, we thank our families for being patient and supportive throughout many evenings and weekends of working on the journal.

CAROLYN CALLAGHAN
Editor in Chief

and

TRINA RYTWINSKI
Assistant Editor

Notes *(continued)*

Book Reviews

News and Comment

Mailing date of the previous issue 127(4): 26 March 2014

THE CANADIAN FIELD-NATURALIST Volume 128, Number 2 2014

Articles

Notes

(continued on inside back cover)

ISSN 0008-3550

The CANADIAN FIELD-NATURALIST

Published by THE OTTAWA FIELD-NATURALISTS' CLUB, Ottawa, Canada

Volume 128, Number 3 July–September 2014

COVER: Lake Charr (*Salvelinus namaycush*) in spawning condition on Great Bear Lake, NT August 2007. Photo: Andrew Muir. See Note on anadromous migration Harris *et al.* on pages 260–264 in this issue.

The Canadian Field-Naturalist

Volume 128, Number 3 July–September 2014

Home Range, Movements, and Denning Chronology of the Grizzly Bear (*Ursus arctos*) in West-Central Alberta

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Graham, Karen, and Gordon B. Stenhouse. 2014. Home range, movements, and denning chronology of the Grizzly Bear (*Ursus arctos*) in west-central Alberta. Canadian Field-Naturalist 128(3): 223–234.

An understanding of the natural history of the Grizzly Bear (*Ursus arctos*) is important for recovery planning. We present data on home range size, movements and denning chronology collected using Global Positioning System (GPS) collars on Grizzly Bears in west-central Alberta. Mean annual kernel estimates for adult (1034 ± 656 (SD) km^2) and subadult (1298 ± 1207 km^2) males were larger than those for females with cubs of the year (213 ± 212 km^2) and lone adult females (337 ± 176 km^2) but not different from sub-adult females, females with yearlings, or females with ≥ 2-yr old cubs ($P > 0.05$). Mean rates of movement among female age–reproductive classes were different from each other ($Z_0 < 2.70$, $P > 0.05$) but not different from sub-adult males ($Z_0 < 2.70$, $P > 0.05$). Rates of movement of adult males were significantly different only from those of females with cubs of the year ($Z_0 = 3.94$, $P = 0.001$). The greatest amount of movement occurred in June and the least in October. Bears traveled fastest in the morning and evening and slowest at night. Pregnant females had the longest denning period (175 days, ± 16 days SD). No difference was detected in denning duration among the remaining five age–sex–reproductive classes ($P > 0.05$). GPS collars provided large location datasets from which accurate home range estimates, hourly movement rates, and precise denning dates were determined. Examining similarities and differences in the basic biology of Grizzly Bears from various locations will improve our understanding of the plasticity of this species and the potential impacts of habitat and climate change.

Key Words: Grizzly Bear; *Ursus arctos*; home range; movement; denning chronology; GPS collar; Alberta

Introduction

Many populations of the Grizzly Bear (*Ursus arctos*) are at some level of endangerment, and a better understanding of the species' basic biology is important to aid conservation efforts (Servheen 1993; Alberta Sustainable Resource Development 2008*). The collection and collation of biological data from across the range of the Grizzly Bear provides an opportunity to compare current data with those in past studies as well as studies from other areas, so that we might better understand the plasticity and adaptability of this species. Increased knowledge of its basic biology may also increase our ability to predict impacts of landscape change, habitat modification, and climate change on Grizzly Bear populations.

The purpose of this paper is to present information on Grizzly Bear home range size, movements, and denning chronology in west-central Alberta from bears equipped with Global Positioning System (GPS) collars in west-central Alberta. We compare age–sex classes in terms of home range size, movements, and denning chronology. Further, we compare movements during different months and different times of day.

Despite numerous studies of the Grizzly Bear in west-central Alberta addressing specific research topics using GPS collar data (e.g., Nielsen *et al.* 2002, 2003, 2004, 2006, 2010; Munro *et al.* 2006; Berland *et al.* 2008; Roever *et al.* 2008, 2010; Graham *et al.* 2010; Cristescu *et al.* 2011; Northrup *et al.* 2012; Stewart *et al.* 2012), basic biological data on home range, movements and denning chronology have not yet been presented. Earlier studies using Very High Frequency (VHF) radio collars have provided estimates of home range size, movements, and denning chronology; however, improvements in the quality and quantity of location data made possible by GPS collar technology should increase our understanding of these characteristics. We compare our results with those from earlier studies in Alberta that relied on VHF technology, as well as studies throughout the circumpolar range of the Grizzly Bear.

Study Area

We focused on two genetically distinct Grizzly Bear populations in west-central Alberta (Proctor *et al.* 2012): the Yellowhead population unit (YPU; 53°14'53"N, 117°25'12"W) and the Grande Cache population unit (GCPU; 44°10'19"N, 77°13'44"W). The location of the YPU includes southern Jasper National Park in the Rocky Mountains (Figure 1). The GCPU is located directly north of the YPU and covers the northern part of Jasper National Park and the Wilmore Wilderness area, both in the Rocky Mountains (Figure 1). Elevations are highest (up to 2700 m) in the western portion

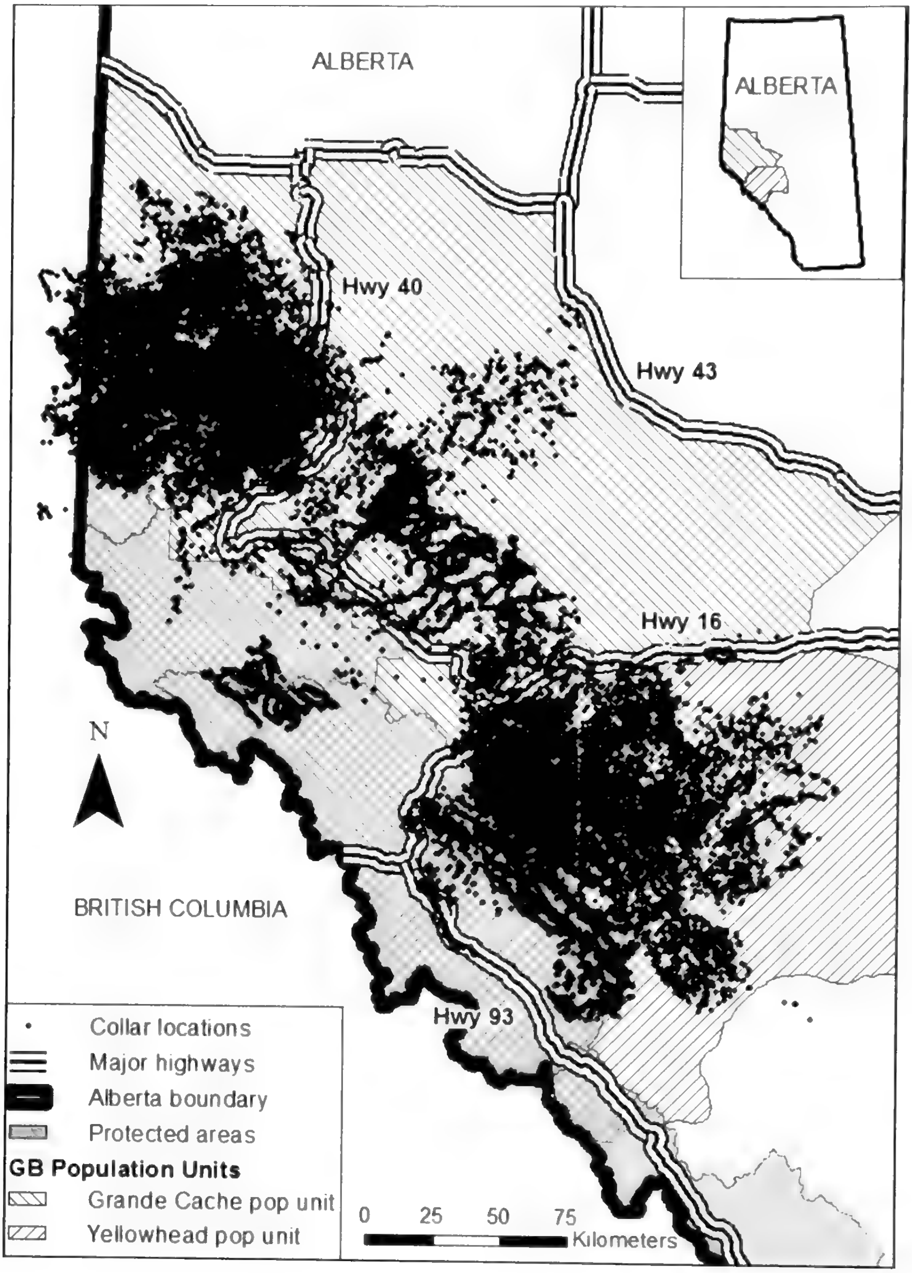

FIGURE 1. Location data for Grizzly Bears (*Ursus arctos*) collected using Global Positioning System collars from 1999 to 2010 for the Yellowhead and Grande Cache population units in west-central Alberta, Canada.

of both areas and decline eastward to approximately 900 m. This elevation gradient results in a diversity of ecosites (Beckingham *et al.* 1996*) including alpine/subalpine meadows; forests dominated by coniferous species consisting of Lodgepole Pine (*Pinus contorta*), White Spruce (*Picea glauca*), Black Spruce (*P. mariana*), or Englemann Spruce (*P. englemannii*); mixed forests comprising conifers with Trembling Aspen (*Populus tremuloides*) or Balsam Poplar (*P. balsamifera*); and wet meadow complexes. Both locations include large cleared areas, seismic lines, pipelines, and roads associated with timber harvesting, oil and gas exploration and development, and open-pit coal mining. A number of recreational activities also occur within these areas, including hunting, trapping, use of all-terrain vehicles, camping, hiking, and mountain biking. A regulated spring hunt for American Black Bears (*Ursus americanus*) occurred during the study. A limited-entry hunt for Grizzly Bears occurred during spring 1999–2005, but ceased in 2006.

Methods

Captures

Grizzly Bears in the YPU and GCPU were captured and radio-collared from 1999 to 2010 and 2003 to 2010, respectively. Capture methods included the use of cul-

vert traps, leg-hold snares, and aerial darting from a helicopter. In 2010, we terminated the use of snares because of potential long-term capture impacts (Cattet *et al.* 2003, 2008). From 2010, capture techniques involved aerial darting and culvert traps with satellite alarm systems, designed to minimize the amount of time bears were confined in the trap. Aerial darting via helicopter occurred in open areas, such as alpine/sub-alpine meadows and logged areas. Most snares and culvert traps were placed in forested areas where aerial darting was not feasible. Sites were usually < 100 m from a road or other access feature type; however, some sites were accessible only by helicopter. Capture protocols were approved by the Canadian Council on Animal Care for the safe handling of bears and approved annually by the University of Saskatchewan and the Government of Alberta animal care committees.

Grizzly Bears were fitted with a GPS radio collars, including Simplex, Tellus, or Tellus Satellite collars (Televilt [now Followit], Lindesberg, Sweden); or Advanced Telemetry Systems (ATS; Isanti, Minnesota, USA) collars. All collars emitted a unique VHF radio signal to locate the bear. From 1999 to 2005, Simplex collars were used and typically programmed to obtain a location every 4 h during the non-denning period. Collars deployed in the spring were retrieved in the fall of the following year (1.5 years later) using a remote drop-off mechanism, which allowed retrieval without the need for recapture. Improvements in Tellus collars and battery life occurred in 2004. The new collars were able to provide hourly locations during the non-denning period over 1.5 years. Remote data downloads were possible for all versions of Televilt collars, allowing data to be obtained even if the collar was not retrieved at the end of its life. In 2010, one bear was collared with a Tellus Satellite GPS collar, and data from this collar were remotely obtained from a service provider. ATS collars were used from 1999 to 2008. As they did not have the remote data retrieval option, collars were retrieved using a remote drop-off mechanism at the end of the battery life, typically 8 months. Grizzly Bears were also fitted with a VHF ear tag transmitter (ATS), so that they could be located for collar removal in case the collar failed.

A premolar tooth was extracted from captured bears and sent to a commercial laboratory for age determination based on cementum annuli counts (Matson *et al.* 1993*). Age classes used in our analysis included adult (≥ 5 years) and independent sub-adult (2 to < 5 years). Bears younger than 2 years were not collared, but were given an ear tag transmitter, for possible relocation and capture in successive years. We recorded whether captured females were accompanied by cubs of the year (COY), yearlings, or older cubs (≥ 2 years old).

Home range

We calculated annual 100% minimum convex polygons (MCP) and 95% kernel home ranges using the program ABODE (Laver 2005*) in a Geographic Information System (GIS). We determined both MCPs and 95% kernels (Worton 1987) to allow comparisons with other studies. Fixed biweight kernels (Sliverman 1986) were calculated using a volume contouring method. We used a least-squares smoothing factor (Seaman and Powell 1996) and a grid cell size of 300 m^2. Kernels were standardized using the unit variance method (Silverman 1986).

We included a home range estimate only if data locations were available from May to October to ensure that the entire year was represented (Arthur and Schwartz 1999; Belant and Follmann 2002; Girard *et al.* 2002). In addition, each home range estimate required a minimum of 100 days of location data or it was excluded from the analysis (Arthur and Schwartz 1999; Belant and Follmann 2002). If a bear generated more than one year of location data for the same age or reproductive class, only the data for the year with the greatest number of locations were used. We determined mean 100% MCP and 95% kernel home range estimates for seven age–sex–reproductive classes: female with COY, female with yearlings, females with ≥ 2 year olds, lone adult females, sub-adult females, sub-adult males, and adult males (Table 1). Only the 95% kernel estimates were statistically compared among the seven age–sex–reproductive classes.

Movement rates

We used Visual Basic in Access Microsoft (version 2003) to determine the distance between successive

TABLE 1. Home range estimates, calculated as mean 100% minimum convex polygons (MCP) and 95% kernels, for Grizzly Bears (*Ursus arctos*) in west-central Alberta, by age–sex–reproductive class based on Global Positioning System collar data. Kernel estimates for classes with different numbered superscripts are statistically different ($P < 0.05$) based on non-parametric multiple comparison tests.

Age–sex–reproductive class	n	Mean annual 100% MCP (SD, range), km^2	Mean annual 95% kernel (SD, range), km^2
Female with COY	11	370 (250, 119–1025)	213 (212, 62–808)^{1}
Female with yearling	9	735 (822, 267–2904)	472 (527, 136–1848)^{1,2}
Female with ≥ 2 year old	7	722 (464, 202–1554)	494 (428, 105–1397)^{1,2}
Sub-adult female	14	732 (376, 222–1447)	394 (231, 86–836)^{1,2}
Lone adult female	22	615 (311, 200–1260)	337 (176, 107–706)^{1}
Sub-adult male	10	2152 (1469, 509–4993)	1298 (1207, 354–4282)^{2}
Adult male	14	1824 (1006, 336–3154)	1034 (656, 203–2071)^{2}

locations and calculate hourly movement rates. We chose 1-h time units because these were our most fine-scaled temporal data and hourly readings were possible after 2004 using improved collars that allowed a collar to last 1.5 years at an hourly fix rate during the non-denning period. We only measured movements outside the denning period because previous research has shown that Grizzly Bear movements are reduced before den entry (Nelson *et al.* 1983; Friebe *et al.* 2001; Manchi and Swenson 2005) and immediately after den exit (Craighead and Craighead 1972; Nelson *et al.* 1983; Schwartz *et al.* 2010). To exclude the denning period, we removed data locations within 500 m of known den sites and within an average of 7 days of den entry and exit dates (see below). Also, the movement of many Grizzly Bears is reduced for up to a month after a capture event (Cattet *et al.* 2008); thus, location data collected within 30 days of a capture were also removed from analysis. For movement rates, we pooled females with yearlings and older cubs into one class (females with yearlings+) to increase sample size and produce six age–sex–reproductive classes.

Denning chronology

We determined den entry and exit dates and time in the den from collar data. Collars were programed to acquire at least one location every day during the denning period because the manufacturer recommended keeping the batteries active rather than shutting them off completely for months at a time. Typically, when bears entered their dens, GPS collars were unable to acquire a location even though an attempt was made; therefore, the day the collar consistently stopped recording locations was considered to be the day the bear entered the den. Den exit dates were determined in a similar fashion, as the day the collar began to signal locations consistently again in the spring. Time in the den was calculated based on data from bears with known entry and exits dates for the same denning period.

Statistical analysis

We tested for normality and homoscedasticity using a Shapiro-Wilk test for normality and a Bartlet's test for equal variances as well as visual examination of standardized normal probability plots. When data were not normal, appropriate transformations were applied or nonparametric analyses were used. We used a Krusal-Wallis test to determine whether mean kernel sizes differed among age–sex–reproductive classes and subsequent nonparametric multiple comparison tests to determine which means were significantly different from others (Zar 1984). We graphed the hourly movement rates for each age–sex–reproductive class by hour of the day and month of the year. We used a mixed effects multiple linear regression on log transformed hourly movement rates with bears as the random effects factor to determine whether movement rates differed across the fixed effect factors of age–sex–reproductive class, activity period, and month. We then conducted multiple comparisons of the marginal means for the fixed effect factors using a Bonferroni adjustment to determine where differences occurred. We used ANOVA to compare den duration across age–sex–reproductive class followed by a Tukey post-hoc multiple comparison to determine which classes were different from others. Statistical analyses were conducted using Stata SE (v. 12.0 for Windows; StataCorp LP, College Station, Texas). We used an alpha level of 0.05.

Between 1999 and 2010, we captured 40 females and 31 males from the YPU and 18 females and 36 males from the GCPU. A total of 251 capture events took place. Individual bears were captured on average 2.5 ± 1.8 times in the YPU and 1.4 ± 0.8 times in the GCPU. A total of 53 Grizzly Bears from the YPU and 46 from the GCPU were collared. Collars functioned on bears from the YPU for an average of 476 ± 445 days, range = 13–2025 days) and 346 days on bears from the GCPU (SD 396 days, range 3–2072 days). In total 659 744 GPS locations were collected during this period.

Home range size

We estimated 97 annual 100% MCP and 95% kernel home range sizes for 59 Grizzly Bears, using location data collected from 1999 to 2010. We included 21 bears more than once because their age or reproductive class changed over time. A mean of 1691 locations (SD 1962, range 203–9804) were used in the MCP and kernel estimates. The mean kernel size across the seven age–sex–reproductive classes differed significantly ($H_6 = 32.31$, $P < 0.001$; Table 1). Kernel sizes of adult and sub-adult males were not significantly different from each other ($P > 0.05$, Table 1) or from those of sub-adult females ($P > 0.05$), females with yearlings ($P > 0.05$) or females with ≥ 2-year-old cubs ($P > 0.05$), but they were significantly larger than females with COY (adult males: $Q_7 = 4.56$, $P < 0.05$; sub-adult males: $Q_7 = 4.82$, $P < 0.05$) and lone adult females (adult males: $Q_7 = 3.33$, $P < 0.05$; sub-adult males: $Q_7 = 3.64$, $P < 0.05$). There were no differences in home range size among the five female age–reproductive classes ($P > 0.05$, Table 1).

Movements

Hourly location data from 39 Grizzly Bears in the YPU and GCPU provided 87 959 hourly movement rates. Except for females with COY, mean movement rates for all other age–sex–reproductive classes tended to be greatest in June; the greatest movement rates for females with COY occurred in August (Figure 2). Movement rates generally declined after June, although adult males showed an increase in September and October (Figure 2). Movement rates by hour of the day showed a bimodal pattern, with four distinct activity periods (Figure 3). Bears travel slowly at night (2200–0500), quicker during the morning (0600–1100) and evening (1700–2100), and moderately in the afternoon (1200–1600). These four activity periods were used in the regression analysis.

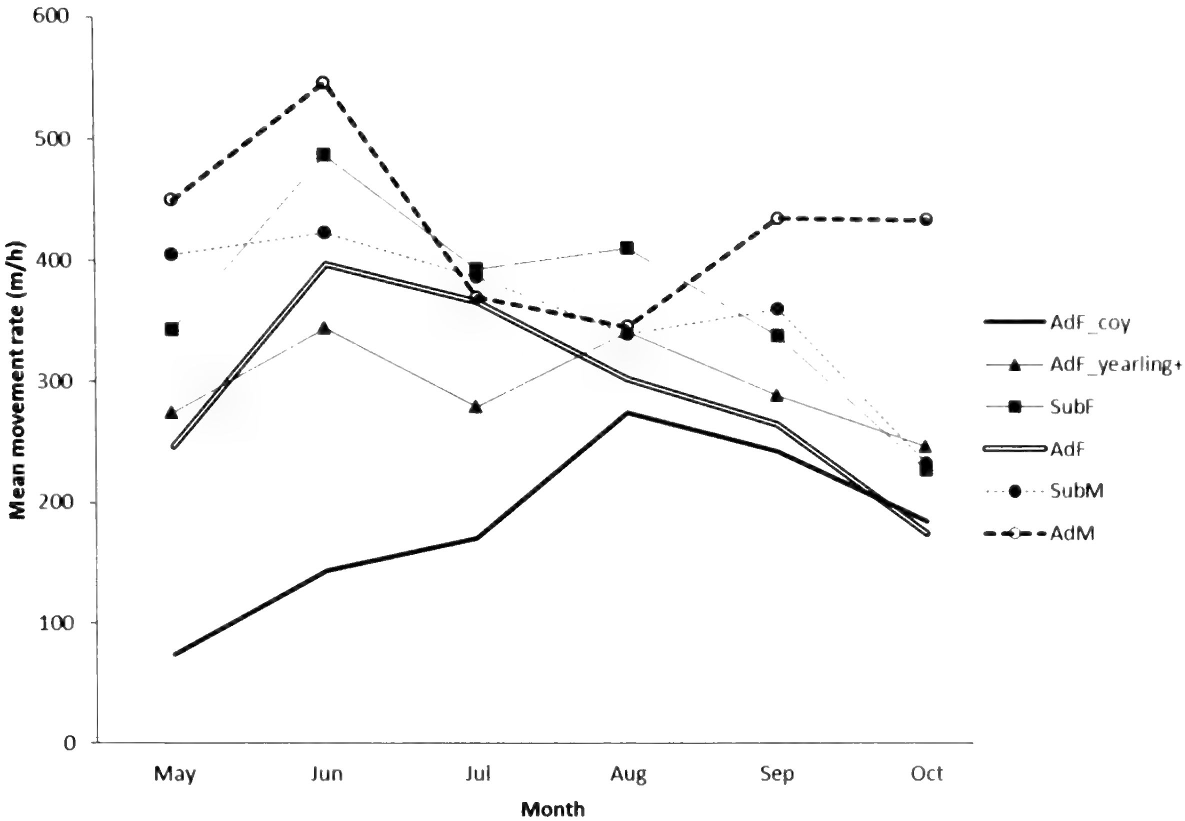

FIGURE 2. Mean rates of movement by month for six age sex reproductive classes of Grizzly Bears (*Ursus arctos*) in west-central Alberta. AdF_coy = females with cub of the year, AdF_yearling+ = females with yearling or older cub, SubF = sub-adult females, AdF = lone adult females, SubM = sub-adult males, AdM = adult males.

TABLE 2. Results for the fixed effect factors (age sex–reproductive class, month and activity period) used in the multiple linear regression analysis to explain hourly movement rates (grouped by bear). Lone adult females, the month of May and the morning activity period were reference categories. Data were log transformed to accentuate heteroscedasticity.

Factor	Age–sex–reproductive class	Coefficient	Standard deviation	Z	$P > \|z\|$	95% confidence interval	
Class	Female with coy	−0.0742	0.0128	−5.79	0.000	−0.0993	−0.04905
	Female with yearling+	0.0419	0.0105	3.96	0.000	0.0211	0.0626
	Sub-adult female	0.1293	0.0098	13.22	0.000	0.1101	0.1485
	Sub-adult male	0.0157	0.0415	0.38	0.704	−0.0655	0.0970
	Adult male	0.0839	0.0390	2.15	0.032	0.0074	0.1604
Month	June	0.1291	0.0099	13.03	0.000	0.1097	0.1486
	July	0.1858	0.0091	20.46	0.000	0.1680	0.2036
	August	0.1578	0.0091	17.28	0.000	0.1399	0.1756
	September	0.0680	0.0093	7.29	0.000	0.0497	0.0863
	October	−0.1326	0.0091	−14.55	0.000	0.1505	−0.1147
Activity period	Afternoon	−0.1606	0.0068	23.55	0.000	0.1740	−0.1473
	Evening	0.0828	0.0068	12.17	0.000	0.0694	0.0961
	Night	−0.5367	0.0062	−86.19	0.000	0.5489	−0.5245
Intercept		2.0634	0.0261	79.09	0.000	2.0122	2.114

Age–sex–reproductive class (six classes), activity period (morning, afternoon, evening, and night) and month (May to October) were significant predictors of hourly movement rates (Tables 2 and 3). Comparison of marginal means indicated that all 6 months were significantly different from each other ($Z_9 < 40.57$, $P \leq 0.01$ for all 15 comparisons; Table 4). The fastest mean movement rate occurred in June and the slowest in October. Likewise, all four activity periods were significantly different from each other ($Z_2 < 94.88$, $P < 0.01$ for all six comparisons; Table 5). Bears moved fastest in the evening followed by the morning and afternoon, with the slowest mean movement rate occurring at night.

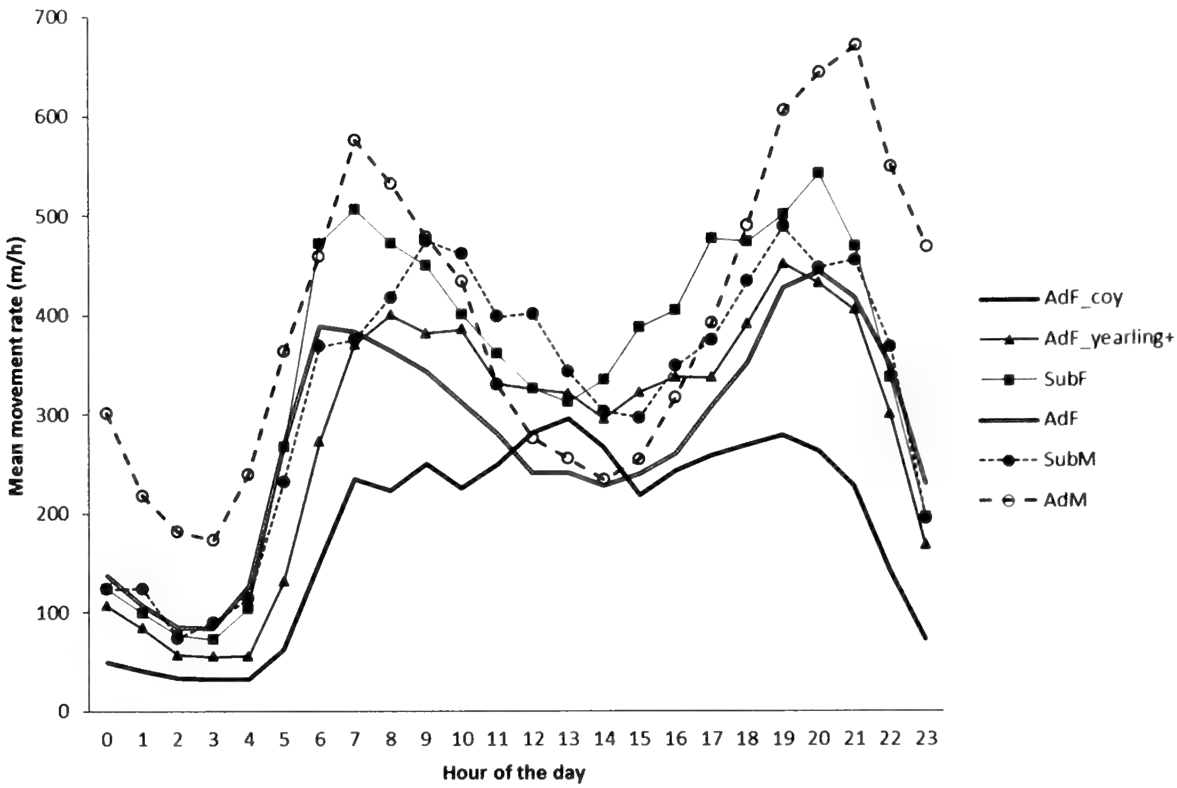

FIGURE 3. Mean rates of movement by hour of the day for six age-sex-reproductive classes of Grizzly Bears (*Ursus arctos*) in west-central Alberta. AdF_coy = females with cub of the year, AdF_yearling+ = females with yearling or older cub, SubF = sub-adult females, AdF = lone adult females, SubM = sub-adult males, AdM = adult males.

TABLE 3. Results for bear as the random effect factors used in the multiple linear regression analysis to explain hourly movement rates. Data were log transformed to accentuate heteroscedasticity.

Random effects for bear	Estimate	Standard deviation	95% confidence interval
Standard deviation of intercept	0.1117	0.0139	0.0874–0.1426
Standard deviation of residuals	0.6903	0.0016	0.6871–0.6935

TABLE 4. Mean hourly movement rates of Grizzly Bears (*Ursus arctos*) in west-central Alberta by month. Post-hoc comparisons with Bonferroni adjusted P values are provided.

Month	n	Mean movement rate, m/h (SD)*	June	July	August	September	October
May	10 657	287 (487.7)	$Z_9 = 13.03$ $P < 0.001$	$Z_9 = 20.46$ $P < 0.001$	$Z_9 = 17.28$ $P < 0.001$	$Z_9 = 7.29$ $P < 0.001$	$Z_9 = -14.55$ $P < 0.001$
June	10 298	391 (602.3)		$Z_9 = 6.39$ $P < 0.001$	$Z_9 = 3.19$ $P = 0.001$	$Z_9 = -6.63$ $P < 0.001$	$Z_9 = -28.38$ $P < 0.001$
July	17 429	346 (473.5)			$Z_9 = -3.78$ $P < 0.001$	$Z_9 = -15.14$ $P < 0.001$	$Z_9 = -40.57$ $P < 0.001$
August	18 132	343 (478.9)				$Z_9 = -11.76$ $P < 0.001$	$Z_9 = -37.54$ $P < 0.001$
September	15 461	320 (497.7)					$Z_9 = -25.05$ $P < 0.001$
October	15 982	251 (497.8)					

*SD = standard deviation.

TABLE 5. Mean hourly movement rates of Grizzly Bears (*Ursus arctos*) in west-central Alberta by activity period. Post-hoc comparisons with Bonferroni adjusted P values are provided.

Activity period	n	Mean movement rate, m/h (SD)*	Afternoon	Evening	Night
Morning	22 526	403 (541.8)	$Z_9 = -23.55$ $P < 0.001$	$Z_9 = 12.17$ $P < 0.001$	$Z_9 = 86.19$ $P < 0.001$
Afternoon	18 863	296 (447.3)		$Z_9 = -34.28$ $P < 0.001$	$Z_9 = 57.29$ $P < 0.001$
Evening	19 032	448 (563.7			$Z_9 = -94.88$ $P < 0.001$
Night	27 538	185 (420.7)			

*SD = standard deviation.

TABLE 6. Mean hourly movement rates of Grizzly Bears (*Ursus arctos*) in west-central Alberta, by age sex reproductive class. Post-hoc comparisons with Bonferroni adjusted P values are provided. Non-significant ($P > 0.05$) differences are in bold.

Age–sex - reproductive class	n	Mean movement rate, m/h (SD)*	Female with yearling+	Sub-adult female	Lone adult female	Sub-adult male	Adult male
Female with COY	7 354	191 (317.8)	$Z_9 = 9.28$ $P < 0.001$	$Z_9 = 12.69$ $P < 0.001$	$Z_9 = -5.79$ $P < 0.001$	**$Z_9 = 2.12$** **$P = 0.515$**	$Z_9 = 3.94$ $P = 0.001$
Female with yearling+	14 645	297 (449.6)		$Z_9 = 6.12$ $P < 0.001$	$Z_9 = 3.96$ $P = 0.001$	**$Z_9 = -0.62$** **$P = 1.000$**	**$Z_9 = 1.06$** **$P = 1.000$**
Sub-adult female	15 048	366 (506.4)			$Z_9 = 13.22$ $P < 0.001$	**$Z_9 = -2.70$** **$P = 0.102$**	**$Z_9 = -1.14$** **$P = 1.000$**
Lone adult female	28 160	292 (459.6)				**$Z_9 = 0.38$** **$P = 1.00$**	**$Z_9 = 2.15$** **$P = 0.47$**
Sub-adult male	7 584	342 (522.3)					**$Z_9 = -2.63$** **$P = 0.128$**
Adult male	15 168	408 (649.7)					

*SD = standard deviation.

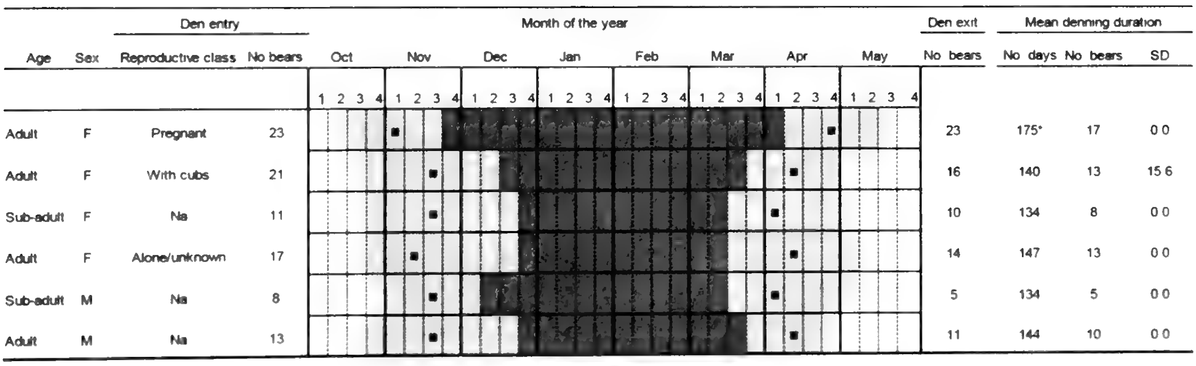

FIGURE 4. Den entry and exit dates by quarter month and age sex–reproductive class for Grizzly Bears (*Ursus arctos*) in west-central Alberta, determined from Global Positioning System collar data from 1999 to 2010. Small black squares indicate mean den entry or exit dates, light shading indicates the range of entry and exit dates and dark shading indicates when all bears were in their dens. Den time was longer for pregnant females than for the other five classes (Tukey post-hoc multiple comparison test; $P < 0.002$) and is indicated by an asterisk. Females with cubs represent females accompanied with any aged cub at den entry.

Adult males and sub-adult females had the fastest mean movement rates (408 m/h and 366 m/h, respectively) but adult and sub-adult males had the largest standard deviations (650 and 522, respectively; Table 6). Comparisons of marginal means (Table 6) showed that adult males were significantly faster than females with COY ($Z_9 = 3.94$, $P = 0.001$) but not different from the remaining age–sex–reproductive classes ($Z_9 < 2.63$, $P > 0.05$) while sub-adult males were not different from any of the age–sex–reproductive classes ($Z_9 < 2.70$, $P > 0.05$). Females with COY had the slowest movement rate, followed by lone adult females, females with yearlings, and older and sub-adult females; all which were significantly different from each other ($Z_9 > 3.94$, $P < 0.01$).

Denning

Different age–sex classes exhibited different denning chronology (Figure 4). Pregnant females entered dens first, in early November, followed by lone adult females, females with cubs of all ages and adult males in close succession. Sub-adult males and females entered their dens last, in late November (Figure 3). Conversely, Grizzly Bears exited their dens in the reverse order with sub-adult males and females emerging first, in early April, followed by adult males, females with yearlings or older, lone adult females, and finally, females with COY, in late April. Denning duration varied among age–sex–reproductive class ($F_{5,60}$ = 8.78; $P < 0.001$). Pregnant females had the longest denning duration, significantly longer than lone adult females ($q_{60,6} = -4.04$, $P = 0.002$), females with yearlings and older ($q_{60,6} = -4.99$, $P < 0.001$), adult males ($q_{60,6} = -4.17$; $P = 0.001$), sub-adult females ($q_{60,6} = -5.04$, $P < 0.001$), and sub-adult males ($q_{60,6} = -4.27$; $P = 0.001$). There were no significant differences in length of denning duration among the other age–sex–reproductive classes ($P > 0.05$). Pregnant females spent the longest time in dens, (approximately 48% of the year), whereas sub-adults of both sexes spent the least amount of time in dens, approximately 38% of the year) (Figure 3).

Discussion

The age and sex of a Grizzly Bear are important factors influencing home range size and rates of movement throughout their circumpolar range (Pearson 1975*; Blanchard and Knight 1991; Mace and Waller 1997; McLoughlin *et al.* 1999; Dahle and Swenson 2003a; Stevens and Gibeau 2005; Ciarniello *et al.* 2009; Edwards *et al.* 2009). Adult males typically have large home ranges and move quickly, probably, in part, because they are searching for reproductive females (Blanchard and Knight 1991; Dahle and Swenson 2003a; Krofel *et al.* 2010). Our results support this searching behaviour: the fastest movements by adult males occurred in June, which corresponds to the peak mating period in our area (Stenhouse *et al.* 2005). Large ranges of movement by adult males have also been explained by individuals travelling more in search of food to support a large body mass (McNab 1963; McLoughlin *et al.* 1999) and this could also be the reason for the increase in movement rates observed among adult males in the fall during our study. Fall is the period of hyperphagia (Nielsen *et al.* 2004); thus, adult males may travel more at this time in search of food to fatten up before denning. Adult males may also be actively gathering information on other bears within their home range for the following year (Dahle and Swenson 2003a). The relatively fast movements of females with yearlings and older cubs compared with those of lone adult females may also be a result of searching for food to satisfy the energy demands of the female and her growing cubs (Blanchard and Knight 1991).

The slow movements of females with COY have been attributed to the reduced mobility of the COY and an avoidance of males to reduce possible infanticide (Blanchard and Knight 1991; Dahle and Swenson 2003a,b; Steyaert 2012). However, home range size of females with COY was not significantly different from that of other female age–reproductive classes. This is in contrast to findings for Grizzly Bears in Sweden (Dahle and Swenson 2003a), but similar to those in the Northwest Territories (McLoughlin *et al.* 1999). Dahle and Swenson (2003b) found that spring ranges of females with COY in Sweden were small, but expanded once the breeding season was over. Although we did not examine seasonal ranges, our mean monthly movement rates suggested that movements increased each month until August when rates were similar to those of lone adult females. We cannot say whether movement rates in May were slow because of limited COY mobility or to avoid infanticidal males, but home ranges of females with COY likely expand throughout the summer until they are similar in size to those of other female age–reproductive classes.

Our home range estimates for male and female sub-adults were based on whether the bear was independent and < 5 years of age. Because we did not distinguish between dispersing and philopatric individuals, our estimates likely included dispersing bears and, therefore, did not conform to the traditional definition of a home range (Burt 1943). Because sub-adult males disperse farther than sub-adult females (Blanchard and Knight 1991; Zedrosser *et al.* 2007), the likely inclusion of dispersing males resulted in a large home range estimate and standard deviation and could explain why our estimate was four times larger than the home range reported for philopatric sub-adult males in Sweden (Dahle *et al.* 2006).

The large variation in hourly movement rates by adult and sub-adult males and the conservative nature of the Bonferroni adjustment (Garcia 2004) could have resulted in missing significant differences (Type II error). The mean movement rate of sub-adult males was not different from the other age–sex–reproductive classes, and adult males' rate was only different from that of females with COY. Other researchers have documented differences in movement rates between the sexes (Blanchard and Knight 1991, McLoughlin *et al.* 1999). Perhaps of more interest is the large variability we found in male movement rates. Further work to look at movements by males and site visits to areas where different movement rates occurred are needed to understanding the observed differences.

The bimodal activity pattern displayed by Grizzly Bears in our study was similar to that reported for British Columbia (McCann 1991), Montana (Aune and Kasworm 1989*), and Europe (Roth 1983; Roth and

Huber 1986; Moe *et al.* 2007), but the mid-day inactive period was longer and appeared to be the main rest period for the European bears. In contrast, male Grizzly Bears in Wyoming were active throughout the night and rested in mid-afternoon while females showed a pattern similar to our adult females (Holm *et al.* 1999). Movement can be influenced by many factors including season, cover, temperature, food availability, age, sex, bear density, and human activities (Aune and Kasworm 1989*; McCann 1991; Dahle *et al.* 2006). In the future, the ability to compare movements with data of similar quality and quantity within a population over time and across populations may help us to better understand factors that influence movement rates.

Three studies conducted more than a decade ago within our study area also reported home range estimates (Pearson and Nolan 1976*; Russell *et al.* 1978*, 1979*; Horejsi and Stegenga 1981*; Horejsi and Slatter 1982*; Horejsi and Raine 1983*; Nagy *et al.* 1989*; Nagy and Haroldson 1990). These studies, which relied on VHF collars to obtain a location on a weekly or biweekly schedule, provided the foundation of our understanding of Grizzly Bear biology in Alberta. VHF-based home range estimates were typically based on < 50 locations and bear locations were likely missed when the animal had moved outside the survey area (Russell *et al.* 1979,* Dahle and Swenson 2003a, Collin *et al.* 2005); therefore, these studies likely underestimated the true home range size (Arthur and Schwartz 1999; Girard *et al.* 2002). However, similar to our results, their data showed that male bears were fast moving, MCPs for males were larger than those for females, and females with COY had the smallest MCPs.

Denning is believed to have evolved as a mechanism to endure periods with little food (Manchi and Swenson 2005); however, the triggers that cause a Grizzly Bear to enter and leave a den are not fully understood (Friebe *et al.* 2001). On a large scale, latitude explains some of the variability in denning period across the Grizzly Bear's range (Manchi and Swenson 2005): in Sweden (Manchi and Swenson 2005) and the Canadian north (McLoughlin *et al.* 2002) Grizzly Bears denned 10–30 days longer than in west-central Alberta, whereas, in Yellowstone, den time was 10–30 days shorter (Judd *et al.* 1986). However, latitude alone cannot explain all the differences in denning period as some Grizzly Bears on Kodiak Island, Alaska, do not den at all (Van Daele *et al.* 1989), and Grizzly Bears in British Columbia, at a latitude similar to that of our study area, denned more than 50 days longer (Ciarniello *et al.* 2005). Heavy snowfall (Craighead and Craighead 1972; Servheen and Klaver 1983; Friebe *et al.* 2001; Manchi and Swenson 2005) has been associated with den entry for some populations, while declines in food supply may have influenced den entry in others (Clevenger *et al.* 1990; Ciarniello *et al.* 2009). Precise denning dates, along with local weather and snow conditions, body condition, and food supply information, are needed to improve understanding of den ecology within and across populations (K. Pigeon, unpublished data).

Denning duration has been related to a bear's fat stores prior to denning, its surface volume ratio, den type, and reproductive status (Craighead and Craighead 1972; Schwartz *et al.* 1987; Ciarniello *et al.* 2005; Friebe *et al.* 2001; Manchi and Swenson 2005). A long denning duration for pregnant females has been documented for Grizzly Bears throughout their circumpolar range (Craighead and Craighead 1972; Ballard *et al.* 1982; Ciarniello *et al.* 2005; Friebe *et al.* 2001; Manchi and Swenson 2005). Early den entry by pregnant females may have more to do with reproductive physiology than environmental factors (Hissa *et al.* 1994; Friebe *et al.* 2001), and late den exit by females with COY may be a result of waiting until travel conditions are suitable for very young bears (Craighead and Craighead 1972). Small, young male bears had a longer denning duration than old, large males in southern Sweden (Manchi and Swenson 2005), while subadult females had a shorter denning duration than adult females (Friebe *et al.* 2001). We did not find a difference in denning duration among our sub-adults and adults. However, the sample size for sub-adult males was small and post-hoc multiple comparisons can increase the chance of conducting a Type II error (Zar 1984). Therefore, it is possible that we failed to recognize a significant difference among some age–sex–reproductive classes. Further work to examine the denning biology of Grizzly Bears in Alberta is currently underway.

Denning dates from the VHF studies that overlapped our study area were available for Jasper National Park (Russell *et al.* 1979*) and the Wapiti River area (Horejsi and Raine 1983*). These dates were often inexact, and denning duration was difficult to determine when spring and fall monitoring flights were missed due to inclement weather. However, even with inexact dates, researchers conducting the VHF-based studies detected a chronological order for entering and exiting dens that was similar to our findings decades later (Russell *et al.* 1979*; Horejsi and Raine 1983*). GPS collars allowed us to determine precise denning dates and should allow researchers to identify changes in denning duration that may be important for detecting impacts of climate change on Grizzly Bear den biology in the future.

Conservation implications

GPS collars allowed biologists to collect large datasets on movements of individual bears, to determine accurate estimates for home range, and to determine hourly movement rates and precise denning dates. These data permit biologists to compare the biology of the Grizzly Bear across its range and test hypotheses not possible with VHF data. Although VHF-based studies provided home range estimates, they could under-

estimate the true area and movement data were limited. Denning chronology by age–sex–reproductive class was recognized in VHF-based studies, but precise dates were lacking. VHF-based studies required biologists to locate their animals visually, which often involving dangerous low-level flying, but offered opportunities for direct observations. GPS collars provide accurate and abundant data, but ethological observations are often minimal. Observations of individual animals and site visits to GPS locations are crucial for interpreting GPS telemetry data and should be an important component of any research project that employs GPS collars on wildlife.

Acknowledgements

Our study was supported financially by the numerous partners of the Foothills Research Grizzly Bear Program, which includes oil and gas industry partners, forest industry partners, the Alberta government, and the Government of Canada, as well as various non-governmental organizations. We thank the bear biologists and veterinarians who captured and collared Grizzly Bears over the years and those who collected GPS data on the ground and in the air. We also recognize the many highly skilled pilots who continued to bring us home safely after each data collection flight. We thank Julie Duval for maintaining our ever-growing Grizzly Bear database. Thank you to Karine Pigeon, PhD Candidate at Laval University, in association with the Foothills Research Institute for her comments in the denning section of this paper.Thanks to T. Jung and an anonymous reviewer for the helpful and thoughtful suggestions regarding drafts of this paper.

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Received 13 February 2013
Accepted 1 October 2013

Mortality of Common Eider, *Somateria mollissima* (Linnaeus, 1758), and other Water Birds during two Inshore Oiling Events in Southeastern Newfoundland, 2005 and 2006

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Robertson, Gregory J., Scott G. Gilliland, Pierre C. Ryan, Johanne Dussureault, Kyran Power, and Bruce C. Turner. 2014. Mortality of Common Eider, *Somateria mollissima* (Linnaeus, 1758), and other water birds during two inshore oiling events in southeastern Newfoundland, 2005 and 2006. Canadian Field-Naturalist 128(3): 235–242.

Although the waters off Newfoundland harbour millions of wintering marine birds, chronic marine oil pollution has been repeatedly reported. Unusually high numbers (hundreds) of oiled birds were noted following two events in March 2005 and April 2006 in southeastern Newfoundland. Common Eiders (*Somateria mollissima* [Linnaeus, 1758]) were the main victims in the first event, with at least 1400 affected, based on retrieval of carcasses and aerial surveys. The April 2006 event affected 19 species; Common Eiders were again the most numerous with a minimum of 337 birds oiled. Among the Common Eiders affected in both events, most were the northern type, including the *borealis* (C. L. Brehm, 1824) subspecies and presumed intergrades between *borealis* and *dresseri* Sharpe, 1871. Coupled with the legal harvest, these oiling events may have had an effect on the wintering Common Eider population. Alcids, other sea ducks, loons and gulls were also oiled, but in low numbers (< 100); thus, their populations were not likely affected by these events.

Key Words: Oil pollution; Common Eider; *Somateria mollissima*; water birds; Avalon Peninsula; Newfoundland

Introduction

The cold, productive waters off Newfoundland and Labrador, Canada, are home to large populations of breeding and wintering marine birds (Lock *et al.* 1994). However, chronic oiling problems have been documented in the coastal waters of Newfoundland (Wiese and Ryan 2003), likely because of the large numbers of ships that transit these waters. Although murres (*Uria* spp.) and Dovekies (*Alle alle* [Linnaeus, 1758]) are most severely affected by oiling, other species, including sea ducks, are also found (Wiese and Ryan 2003). Among the coastal wintering species, the Common Eider (*Somateria mollissima* [Linnaeus, 1758]) is the most numerous and also an important game bird in Newfoundland (Wendt and Silieff 1986; Gilliland and Robertson 2009). Unlike pelagic seabirds, which tend to be widely distributed, Common Eiders may form dense flocks, and a single oiling event can affect a large component of the population. Oil spills affecting Common Eiders have occurred in Atlantic Canadian waters in the past (Brown *et al.* 1973).

Two significant events involving hundreds of oiled coastal birds occurred from late February to early April 2005 and April 2006 in southeastern Newfoundland (a third event in November 2004 involving mostly pelagic species is described elsewhere [Robertson *et al.* 2006]). In this paper, we present information from a variety of surveys conducted to assess the geographic scope of these incidents and estimate the number of eiders and other water birds at risk and actually oiled from these spills. To help understand potential effects on populations, we present information on oiled carcasses to assess the population structure and affinities of birds killed. Finally, we evaluate the potential effect of these two oiling events on eiders and other water birds wintering in Newfoundland.

Study Area and Methods

March 2005 incident

On Saturday, 26 February 2005, wildlife officials and pollution prevention officers received reports that oiled eiders were being taken during the legal hunt. Further reports were received on Monday, 28 February 2005, the final day of the open hunting season for sea ducks in Newfoundland. On 1 March, an experienced observer (S.G.G.) used a Canadian Coast Guard helicopter (BO-105, Bölkow, Stuttgart, Germany) to survey the east coast of the Avalon Peninsula from Cape St. Francis to Cape Race (Figure 1) and count the number of eiders at risk in the area and visibly oiled eiders. The survey began and ended at Cape St. Francis, beginning at 1030 and ending at 1345. Survey conditions were excellent: light easterly winds, clear sky, and a temperature of −5°C. The flight track and all observations were recorded using United States Fish and Wildlife Service Global Positioning System Voice Software.

During the initial flight, from north to south at 500 m above sea level, the size and location of all large flocks of eiders and Black-legged Kittiwakes (*Rissa tridactyla* [Linnaeus, 1758]) were recorded. On the return flight,

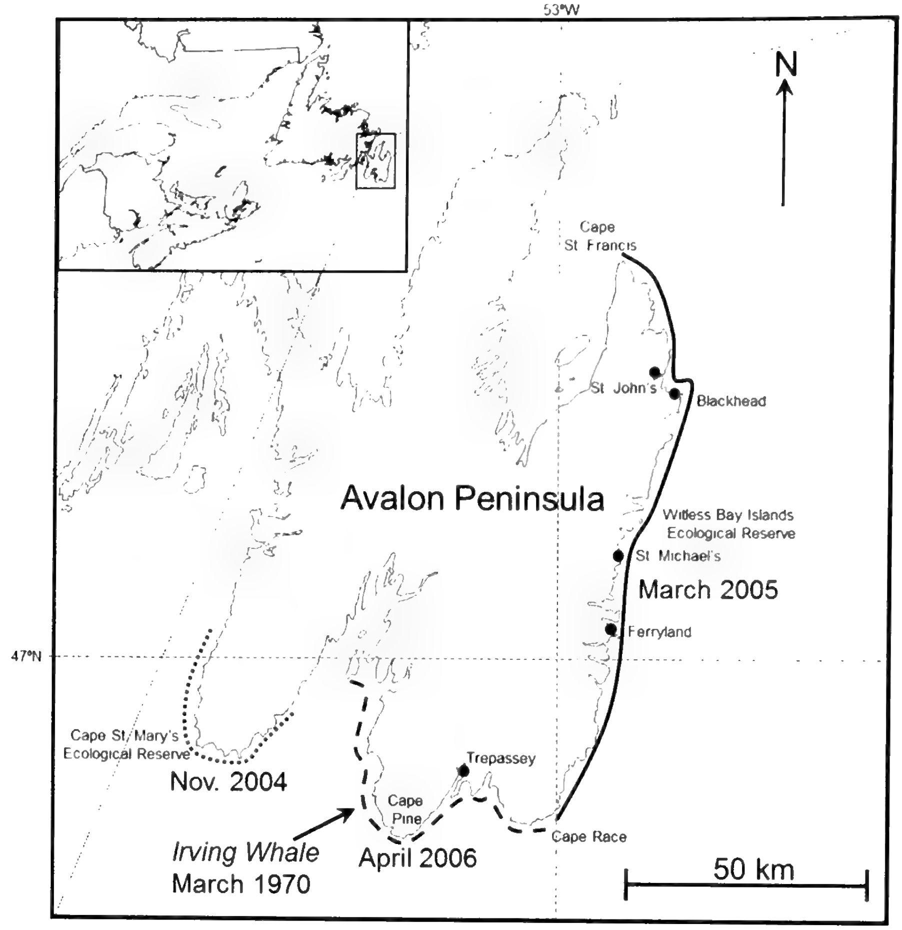

FIGURE 1. Extent of two oiling events in southeastern Newfoundland, March 2005 (solid line) and April 2006 (dashed line). The locations of two other events mentioned in the text are also shown: *Irving Whale*, March 1970 (arrow; Brown *et al.* 1973) and November 2004 (dotted line; Robertson *et al.* 2006).

the focus was on birds that may have been oiled. This survey was conducted from south to north at 35 m above sea level, and the number of eiders loafing on beaches and rocks was recorded; in some cases oiling was visibly apparent on these birds. The number and location of Bald Eagles (*Haliaeetus leucocephalus* [Linnaeus, 1766]) that appeared to be scavenging oiled eiders was also noted.

On 6 March 2005, a second survey was conducted specifically to count the number of eiders that appeared oiled. This survey included simultaneous air and ground counts to correct for observer bias in estimating flock sizes (see Bordage *et al.* 1998) and to determine whether eiders were indeed oiled. Fifteen ground count sites were identified at 4 locations: Cape St. Francis, Blackhead, St. Michael's, and Ferryland (Figure 1). On 5 March 2005, the primary helicopter surveyor (S.G.G.) visited the ground sites with each observer, who would be counting eiders the next day, to ensure that the same geographic areas were being assessed simultaneously from the air and the ground. Observers on the ground counted eiders every 30 minutes at their site. As it was apparent that eiders flushed with the arrival of the helicopter, the previous count was used. Helicopter survey protocols were similar to those used on the return portion of the 1 March survey, except a 206 LR (Bell Helicopter Trextron Canada Ltd, Mirabel, Quebec, Canada) from Universal Helicopters (Goose Bay, Newfoundland and Labrador) was used for the portion of the flight from Logy Bay (near St. John's) to Cape Bonavista (48°42'N, 53°05'W) to the north. The flight ran south to north and took place from 0850 to 1430. Survey conditions again were generally good: light winds, clear sky, and −12°C; however visibility was restricted by local snow squalls. The ratio of ground count to aerial count was calculated for each site where birds were present, and the mean of those ratios was used to correct the aerial counts.

From 26 February to 7 April 2005, crews searched beaches daily for oiled bird carcasses. In addition, birds (and parts) were received from the public, mostly hunters, in late February.

We examined all carcasses received, recording the species, sex, age where possible, degree of scavenging, and degree of oiling. We measured body mass and commonly recorded morphometrics (wing, tarsus, and culmen length) of intact carcasses. For Common Eiders, we also measured aspects of the bill used in subspecific identification (Mendall 1986) and assessed visually whether the bird was *borealis*, *dresseri* Sharpe, 1871, or an intergrade between these subspecies based on bill shape and colouration (Goudie *et al.* 2000). Given the uncertainty of distinguishing the *borealis* subspecies from intergrades, the category "northern-type common eider," which included *borealis* and intergrades, was used (Gilliland and Robertson 2009). To determine whether oiled eiders had lost body condition before being found, we measured the body mass of 60 Common Eiders shot between December 2004 and February 2005 near Point Lance, Newfoundland (near Cape St. Mary's) to compare with the mass of oiled carcasses. Even though this sample was collected earlier in the winter than the oiled birds, they should be comparable as northern Common Eiders do not show strong seasonality in body mass dynamics during the winter (Jamieson *et al.* 2006).

April 2006 incident

On 9 April 2006, reports were received from the public of oiled birds, including gulls, auks, and Long-tailed Ducks (*Clangula hyemalis* [Linnaeus, 1758]) sighted along the southeast coast of the Avalon Peninsula, near Cape Pine and the town of Trepassey (Figure 1). Response teams were deployed to examine beaches from 10 to 18 April. On 12 April, two observers (S.G.G. and G.J.R.) conducted a shoreline survey in a 206 LR helicopter to look for oiled sea ducks, following protocols similar to those described for the March 2005 survey. Skies were clear and survey conditions were very good.

As the birds affected by this oiling event were a varied mix of coastal and pelagic species, a minimum number for each affected species was derived from a variety of sources: for waterfowl, the birds counted on shore on 12 April and any carcasses collected before that date were summed; for species not well assessed by aerial surveys, the number of dead carcasses collected, plus reliable observations of oiled birds from areas outside the beaches regularly surveyed were summed. Birds were measured as described above, but a visual assessment of the subspecific status of Common Eiders was not conducted.

Results

March 2005 incident

We estimated that on 1 March 2005, there were approximately 42 000 Common Eiders along the eastern Avalon Peninsula of Newfoundland; this represented a raw count and was not corrected for observer bias. Assuming that all eiders that were hauled out on beaches and rocks were oiled, we estimated the number of oiled eiders at 1165. Major concentrations of birds were located on islands, which are relatively sparse along this coast, with most on the larger islands in the Witless Bay Islands Ecological Reserve (Figure 1). In addition to the eiders, we observed at least two oiled Long-tailed Ducks, and one dead Northern Gannet (*Morus bassanus* [Linnaeus, 1758]). During the 6 March 2005 helicopter survey, we counted 537 oiled eiders along the eastern Avalon Peninsula. Once again, major concentrations were found on the islands of the Witless Bay Islands Ecological Reserve, and extended further north to include Cape St. Francis (Figure 1). In addition to the eiders, we observed at least two oiled Long-tailed Ducks.

We successfully conducted simultaneous air and ground counts at four locations (Table 1). The ground counts were slightly higher than the corresponding aerial counts (ratio 1.07, standard error [SE] 0.14); using this ratio to adjust for errors in the aerial counts, we estimated that 577 (SE 75) eiders may have been affected by oil on 6 March. Based on other casual observations of oiled eiders at sites that were not detected by the helicopter, we believe this is an underestimate.

TABLE 1. Simultaneous aerial and ground counts of oiled Common Eiders (*Somateria mollissima*) at four loafing locations, 6 March 2005, in Newfoundland.

Location (site)	Ground count	Aerial count
Cape St. Francis	84	85
Blackhead	6	0
St. Michael's		
Site 1	1	1
Site 2	0	0
Site 3	0	0
Site 4	22	9
Site 5	0	0
Cribbies	2	2
Ferryland		
Site 1	3	2
Site 2	1	5
Site 3	1	3
Site 4	0	0
Site 5	0	0
Site 6	1	1
Total	121	108

Most of the carcasses retrieved during this incident were Common Eiders, although carcasses of another five species were also retrieved (Table 2). In addition, another four species were seen oiled: Purple Sandpiper (*Calidris maritima* [Brunnich, 1764]), Common Loon (*Gavia immer* [Brunnich, 1764]), American Herring Gull (*Larus smithsonianus* Coues, 1862), and Long-tailed Duck. Based on visual inspection, most eiders found were of the northern (*borealis*) or intermediate-northern type (males: 92%, n = 36; females: 92%, n = 25). However, using Mendall's (1986) key, more males were classified as *dresseri* (42%, n = 36).

TABLE 2. Species and ages of oiled birds collected on beaches or provided by hunters after an oil spill incident in southeastern Newfoundland, March 2005.

	Immature	Adult	Unknown age	Total
Common Eider (*Somateria mollissima*)				
Female	4	29	11	44
Male	16	28	4	48
Thick-billed Murre (*Uria lomvia*)		2	3	5
Dovekie (*Alle alle*)		1		1
Black Guillemot (*Cepphus grylle*)	2		1	3
Great Black-backed Gull (*Larus marinus*)	1		1	2

Of the males, where more specific aging based on plumage was possible, 28 (64%) were found to be adults, 16 (36%) were sub-adults and none were juveniles. Female and male oiled eiders were 15% and 16% lighter, respectively, than eiders shot earlier the same winter (females: oiled 1445 g, SD 133 g, n = 24; unoiled 1694 g, SD 138 g, n = 32; males: oiled 1600 g, SD 218 g, n = 33, unoiled 1904 g, SD 104 g, n = 28). Live oiled eiders were seen well into April 2005 around the eastern Avalon Peninsula, after which eiders left the area on migration, indicating that this species may survive for over a month after oiling.

April 2006 incident

Between 10 and 16 April 2006, 186 oiled carcasses of 11 species were collected on the southeastern tip of the Avalon Peninsula (Table 3, Figure 1). The most common species recovered were sea ducks (Common Eider 18.6%; Long-tailed Ducks 12.9%) and auks (murres 48.4%; Black Guillemots [*Cepphus grylle* (Linnaeus, 758)] 13.4%; Dovekies and Atlantic Puffins [*Fratercula arctica* (Linnaeus, 1758)] 1.1% each). During the 12 April 2006 aerial survey, 409 birds were seen on shore and assessed as oiled: these included 320 Common Eiders, 64 Long-tailed Ducks, 12 loons, 9 murres, 3 Black Guillemots, and a White-winger Scoter (*Melanitta fusca* [Linnaeus, 1758]). The extent of the distribution of Common Eiders presumed oiled was smaller than that seen after the 2005 event (Figure 1). Combining the aerial survey with the carcass recovery data and adding oiled birds seen outside the main area of focus, we estimate that a minimum of 574 birds of 19 species were affected by this spill (Table 4).

Among recovered Common Eiders, 21 of 22 birds were adults (95.5%), but the sex ratio was close to even (18 females of 34 birds, 52.9%) (Table 3). Similarly, among Long-tailed Ducks, 18 of 21 (85.7%) birds were adults, but 20 of 24 birds were male (83.3%). Based

TABLE 3. Species and ages of oiled birds recovered on beaches in southeastern Newfoundland, April 2006.

	Juvenile			Adult			Unknown			
Species	F	M	U	F	M	U	F	M	U	Total
Common Loon (*Gavia immer*)			1	1	1	2			1	6
Northern Fulmar (*Fulmarus glacialis*)						1				1
Common Eider (*Somateria mollissima*)	1			6	15		11	1		34
Long-tailed Duck (*Clangula hyemalis*)		3		3	15		1	2		24
American Herring Gull (*Larus smithsonianus*)									2	2
Common Murre (*Uria aalge*)		2	12	1	1	13			4	33
Thick-billed Murre (*Uria lomvia*)	1		6	5	4	28			2	46
Murre (*Uria* spp.)									11	11
Dovekie (*Alle alle*)									2	2
Black Guillemot (*Cepphus grylle*)	1	1			1	7			15	25
Atlantic Puffin (*Fratercula arctica*)									2	2

Note: F = female, M = male, U = unknown.

TABLE 4. Minimum numbers of birds by species affected by an oiling incident in southeastern Newfoundland, April 2006. Numbers are totals of birds seen ashore during aerial surveys (ducks), found before the aerial survey, found after the survey and not counted during the aerial survey (auks), and oiled birds reported outside the survey area.

Species	Minimum number oiled
Common Eider (*Somateria mollissima*)	337
Murre (*Uria* spp.)	98
Long-tailed Duck (*Clangula hyemalis*)	66
Black Guillemot (*Cepphus grylle*)	29
Loon (*Gavia* spp.)*	23
American Herring Gull (*Larus smithsonianus*)	7
Razorbill (*Alca torda*)	2
Dovekie (*Alle alle*)	2
Great Black-backed Gull (*Larus marinus*)	2
Red-necked Grebe (*Podiceps grisegena*)	1
Northern Fulmar (*Fulmarus glacialis*)	1
King Eider (*Somateria spectabilis*)	1
White-winged Scoter (*Melanitta fusca*)	1
Purple Sandpiper (*Calidris maritima*)	1
Atlantic Puffin (*Fratercula arctica*)	1
Ring-billed Gull (*Larus delawarensis*)	1
Glaucous Gull (*Larus hyperboreus*)	1
Total	574

*Includes Common (*Gavia immer*) and Red-throated Loon (*G. stellata*).

on Mendall's (1986) subspecific key, three of the 12 female Common Eiders measured were classified as *borealis*, eight as intergrades, and one as *dresseri*. Of the 14 males, six were classified as *borealis*, four as intergrades, and four as *dresseri*. All five of the birds classified as *dresseri* had a total culmen length within 1 mm of the range for the intergrade category, and we suspect that these 5 birds were *borealis-dresseri* intergrades. As in the March 2005 incident, the mass of oiled eiders was low: mean for females 1359 g (SD 136 g, range 1145–1479 g, n = 5); mean for males 1585 g (SD 153 g, range 1430–1864 g, n = 6). The mass of oiled male Long-tailed Ducks was 527 g (SD 93 g, range 434–608 g, n = 4) and the one female weighed 675 g.

Of the murres that could be identified to species, 41.8% (33 of 79) were Common Murres (*Uria aalge* [Pontoppidan, 1763]) and 58.2% were Thick-billed Murres (*U. lomvia* [Linnaeus, 1758]). The age ratios were different for the two murre species: 51.7% of Common Murres were older than one year, while 84.1% of Thick-billed Murres were older than one year. The mean body mass of Thick-billed Murres was 711 g (SD 81 g, range 596–822 g, n = 8) and that of Common Murres was 804 g (SD 37 g, range 774–844 g, n = 4). These masses are 26.0% and 21.0% lighter, respectively, than wintering murres collected in Newfoundland in the 2000s (Thick-billed Murres 958 g, n = 113, McFarlane Tranquilla *et al.* [2010]; Common Murres: 1018 g, n = 63). A sufficient sample was available for measurement of adult Thick-billed Murres: wing length 215 mm (SD 6 mm, range 206–231 mm, n = 24); culmen 33.9 mm (SD 2.2 mm, range 30.4–37.7, n = 18).

Discussion

The Avalon Peninsula harbours important concentrations of wintering Common Eiders, especially later in the winter, as birds move south in advance of sea ice formed to the north (Goudie *et al.* 2000) and in early spring when they begin their northern migration. This was certainly the case in March 2005, when we counted 42 000 eiders along the eastern stretch of the peninsula. Sea ice was notably heavy on the northeastern coast of Newfoundland in February 2005, forcing eiders into small open water leads where they were highly vulnerable to hunting or south into more open water. Therefore, large numbers of eiders were expected around southeastern Newfoundland during this winter.

Based on behaviour that was also noted by Brown *et al.* (1973) by eiders involved in the *Irving Whale* incident, we assumed that at least 1165 eiders were oiled. Eiders in unoiled areas flushed well in advance of the aircraft, but birds suspected to be oiled only flushed on close approach or did not flush at all, as was the case among heavily oiled birds hiding in vegetation adjacent to the shoreline (Brown *et al.* 1973). Therefore, the behaviour of oiled eiders appears to be consistent: they remain close to or on shore and do not respond to an approaching aircraft unless it is very close. On this basis, we are reasonably confident in assuming that all eiders found loafing on islands were oiled, and this likely represents a minimum number. Based on our count of 1165 oiled birds on 1 March 2005, plus oiled eiders shot and reported by hunters, at least 1400 eiders were assumed to be oiled, and this number could easily be larger. Fewer (337) oiled Common Eiders were recorded after the April 2006 incident, but again this represents a minimum.

We detected several large aggregations of loafing eiders on the first flight in 2005 (1 March): 55% of all the eiders encountered during this survey were located at five sites with 75–300 birds each, while only 15% occurred in groups of less than 10 birds. We believed that the greatest source of error was our inability to estimate accurately the number of eiders affected from the air, and we followed this survey with a second flight on 6 March 2005 combining independent aerial and ground counts to correct for observer biases in flock estimation (see Bordage *et al.* 1998). However, by the second survey, all but two of the large aggregations had dissipated (the two largest counts of remaining birds were 65 and 85) and the challenge was detecting individuals or small groups of eiders that were distributed across more than 200 km of coastline. In the future, we recommend that aerial assessments be conducted as soon after an incident as possible to count affected birds

when they occur in large aggregations that are easily detected. Ground counts or photographs should be used to correct observer biases in flock estimation. If the birds are widely distributed in small groups, we suggest using double-observer approaches (see Nichols *et al.* 2000) to allow more precise estimates of the number of birds affected.

The reduction in the number of oiled eiders recorded between the 1 March and 6 March 2005 surveys is noteworthy and may have resulted from a number of causes. The first possibility is that birds perished in the interim, although large numbers of carcasses were not noted at these sites during the 6 March survey or during beach surveys. Eiders appeared to show more "normal" behaviour at the time of the 6 March survey; thus, more lightly oiled birds may have been in the water foraging or loafing and would not have been assessed as oiled. If this is the case, assessments of oiled eiders should take place as soon as possible after an incident and before lightly oiled birds adjust and establish a somewhat normal behavioural routine. Clearly more work is needed to understand the behaviour of oiled birds in the wild so that surveys that best reflect the numbers of birds oiled during an event can be implemented.

Among oiled birds, adults predominated in both incidents, especially the April 2006 event. This was also noted by Brown *et al.* (1973) in the *Irving Whale* spill, which occurred in March 1970 in the same general area as the April 2006 spill. Sex ratios were close to one, however, which differs from the male-biased ratio noted by Brown *et al.* (1973). Most Common Eiders found in both incidents were either members of the northern, or *borealis*, subspecies, or presumed intergrades between the northern and American, *dresseri*, subspecies. In fact, most individuals were classified as *borealis-dresseri* intergrades, which are found breeding in central Labrador (Mendall 1986). Pure *borealis* Common Eiders that breed in the eastern Canadian Arctic winter mainly in Greenland, although about a quarter of the population winters off Newfoundland and in the Gulf of St. Lawrence (Mosbech *et al.* 2006). The Common Eider population breeding in Labrador has been growing (Chaulk *et al.* 2005) and is assumed to overwinter exclusively in eastern Canada. In identifying subspecies, we found some discrepancies between visual inspection of eiders and the use of bill morphology to key eiders to subspecies (Mendall 1986). When developing the key, Mendall did not have a large selection of intergrades, especially males, to include in the analysis. Some more work on determining subspecies of Common Eiders, especially in hybrid zones such as Labrador, is still needed.

Common Eiders are popular game birds in Newfoundland and Labrador and Greenland, and concerns have been raised about the harvest levels, which, according to Gilliland *et al.* (2009), ranged from 68 000 to 83 000 northern eiders annually in the two countries. This assessment of harvest levels suggested that if 6500 female *borealis* are taken annually in Canada, the harvest should be sustainable. The 1400 eiders assumed to be oiled in the March 2005 event, of which half were female, would add at least another 11% to the overall winter take, possibly pushing the population into decline for that season (assuming oiling was in addition to natural and hunting mortality). The fact that most oiled eiders were adults — unlike hunted birds, which are largely juveniles (Gilliland and Robertson 2009) — only exacerbates the pressure this event placed on the population.

Recovered carcasses of Common Eiders were somewhat lighter than normal wintering birds, but they were not as emaciated as murres, and living oiled eiders were observed for over a month after the initial oiling event. Therefore, unlike murres and other auks, Common Eiders appear to be able to sustain some level of oiling and survive. Eiders are inshore feeders, foraging in shallow intertidal and subtidal waters. When oiled, eiders, like the auks, come to shore in large numbers, presumably to avoid frigid waters and the risk of hypothermia resulting from oiled plumage. However, food for eiders is readily available close to shore, and eiders can continue to dive, feed, and return quickly to shore. In contrast, auks that come to shore are far removed from their food source and eventually succumb to starvation. Even if oiled birds are unable to forage, Common Eiders, at least females, are adapted to withstand severe loss of body mass (up to 40%) and condition while they incubate their clutch (Parker and Holm 1990). What is not known is the long-term viability of the eiders that were lightly oiled. Even if they survived, future reproductive attempts by these birds may be compromised, as minute levels of hydrocarbons have been shown to severely disrupt or inhibit reproduction (Leighton 1993; Stubblefield *et al.* 1995), and lingering long-term physiological impairment has been shown in birds that were exposed to sub-lethal doses of hydrocarbons (Alonso-Alvarez *et al.* 2007a,b).

The species composition of murres found in the April 2006 incident was similar in some respects, but also differed from those seen in the November 2004 incident (Robertson *et al.* 2006). Common Murres made up a larger proportion of the murres recovered in April 2006, reflecting their prevalence along the south coast of Newfoundland, especially later in the winter season. In spite of the proximity of Common Murre breeding colonies to the affected area (both Cape St. Mary's and Witless Bay Island Ecological Reserves are less than 100 km away), the majority of recovered Common Murres were juveniles. On the other hand, most Thick-billed Murre carcasses were adults, in a proportion comparable to what would be expected in the population at large (Wiese *et al.* 2004). Body masses of both species were lower than expected for wintering birds. However, the mass of Thick-billed Murres was not quite as low as that of starved birds found in

the "seabird wrecks" of 2007 and 2009 when beached dead birds were found to weigh 622 g and 639 g on average, respectively (McFarlane Tranquilla *et al.* 2010), indicating that oiled birds had some remaining body reserves and hypothermia, toxicity of oil, or both, contributes to the death of oiled murres. Wing and culmen measurements were typical of birds breeding in the Northwest Atlantic and similar to those involved in other oiling events (Brown *et al.* 1973; Robertson *et al.* 2006). Of note was the lack of Dovekies, which are a common victim of oiling in Newfoundland waters (Wiese and Ryan 2003; Robertson *et al.* 2006). Possibly Dovekies had begun to move north on migration by the time of the incident in April 2006.

The April 2006 event was noteworthy in terms of the wide variety of avifauna affected: no less than 19 species, including sea ducks, alcids, loons, gulls, and even a sandpiper and a tubenose. This impact is related to both the timing and location of the event. Unlike many parts of southeastern Newfoundland, the southern tip of the Avalon Peninsula has extensive beach habitat in addition to the rockier cliff habitat surrounding most of the peninsula. This habitat diversity leads to a broader avian community. In addition, in mid-April, many species would be congregating for the spring migration, and others would have begun migration. The spill was early enough that the main wintering aggregations of both eiders and murres had not yet left the area, as most of the eiders were of the northern types and Thick-billed Murres dominated among the recovered murre carcasses (both of these species breed north of Newfoundland). Both inshore (ducks, loons) and offshore species (auks, fulmars) were affected, suggesting that this slick likely started somewhere out from shore and was blown inshore.

Between the April 2006 oiling incident and April 2014, there have been no notable (i.e., affecting >10 birds) inshore oiled bird events in Newfoundland from unknown sources, although significant numbers of oiled birds have been found associated with the *M/V Manolis L* wreck on the northeast coast of Newfoundland. Regular long-term beached bird surveys in southeastern Newfoundland are also beginning to show a reduction in the number of oiled birds coming to shore (Wilhelm *et al.* 2009). In 2005, federal legislation was passed in Canada directed at reducing the chronic ship-source oil pollution problem (Elmslie 2006); concomitantly, additional surveillance and enforcement and education programs were put in place to target this issue. Although continued monitoring is warranted, the indications are that a reduction in chronic ship-source oiling, at least in inshore waters off southeastern Newfoundland, is occurring.

Acknowledgements

We thank the many agencies and individuals who assisted in the response to these oiling events. In addition to collating reports and collecting carcasses, the Canadian Coast Guard provided helicopter support for the various surveys. Graham Thomas, the Government of Canada's Environmental Emergencies Programs, and members of the Atlantic Regional Environmental Emergencies Team provided key oversight of these responses. Sabina Wilhelm, François Bolduc, and an anonymous reviewer provided helpful comments on an earlier draft of this manuscript.

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Received 23 January 2014
Accepted 10 March 2014

Impact of the 2012 Drought on Woody Vegetation Invading Alvar Grasslands in the Burnt Lands Alvar, Eastern Ontario

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Catling, Paul M. 2014. Impact of the 2012 drought on woody vegetation invading alvar grasslands in the Burnt Lands Alvar, eastern Ontario. Canadian Field-Naturalist 128(3): 243–249.

Counts of dead and living trees in open alvar indicated that the 2012 drought had a significant impact on the Burnt Lands Alvar in eastern Ontario, with mortality of woody species ranging from 10% to 100% at open alvar sites. The maximum age of dead trees suggested that the most recent drought of similar impact occurred more than 35 years ago, possibly in 1974. Some of the killed junipers were 87–90 years old. All dry periods indicated on a summer rainfall diagram may not be severe enough to kill woody vegetation, but a drought causing an average 50% kill of woody vegetation in open alvar may have occurred at least once every 30 years over the past century. Consequently the encroachment of woody species into alvar grassland appears not to be a threat to this habitat. Open alvar could have existed on the landscape as isolated occurrences since early postglacial times, if the climate fluctuated in the distant past as it has recently. With evidence for drought in a fluctuating climate to maintain the disjunct occurrences of midwestern plant and animal species, these occurrences may be considered as reliable indicators of a more continuous distribution of such species more than 10 000 years ago.

Key Words: alvar; Great Lakes region; eastern Ontario; drought; woody vegetation; succession; Common Juniper; *Juniperus communis*; White Spruce; *Picea glauca*; Eastern White Pine; *Pinus strobus*; Eastern White Cedar; *Thuja occidentalis*

Introduction

Alvar grasslands are naturally open areas of thin soil over flat limestone or marble rock with a more-or-less sparse grass-dominated vegetation with trees absent (Catling and Brownell 1995). Three kinds of predominant alvar grassland are considered to be globally imperiled, meaning that they are "at high risk of extinction or elimination due to restricted range, few populations or occurrences, steep declines, severe threats, or other factors" (Natureserve 2014). Alvar grasslands also contain a diversity of plants and animals, some of which have been evaluated as at risk or susceptible to extirpation (Catling *et al.* 2014), reflecting the fact that these habitats are subject to a variety of threats. Alvar habitats are important with regard to climate change studies, and the grasslands, in particular, are believed to be the only existing analogues of the *Picea* parkland that existed in front of the Wisconsin glacier for hundreds of thousands of years (Webb 1987). Alvars also provide *in situ* protection for native crop relatives and major recreational opportunities (Catling *et al.* 2014).

The survival of alvar grassland in the northern Great Lakes region since the early postglacial period (e.g., Catling and Brownell 1995; Hamilton and Whitcomb 2010) was likely the result of resistance to succession to woodland as a consequence of fire removing trees and shrubs, periodic drought, and a seasonal cycle of drought and flooding (Catling and Brownell 1995; Jones and Reschke 2005). The effects of fire at a number of sites in the Great Lakes region have been reported to range from the creation and maintenance of grasslands to no effect (e.g., Catling and Brownell 1998; Jones and Reschke 2005; Catling 2009), and it has been concluded that, in some situations, fire is "not the primary factor in maintaining open condition" (Jones and Reschke 2005). The seasonal cycle of spring flooding and late summer drought can be seen on an annual basis, but only Stephenson and Herendeen (1986), working at Maxton Plains in northern Michigan, have documented the impact of periodic drought on alvar grassland over a longer term. An opportunity to add to their observations arose with the drought of 2012 when woody vegetation declined on the northern part of the Burnt Lands Alvar in the Ottawa Valley of eastern Ontario. At the end of the summer of 2012, leaves on many of the predominant conifers had turned brown, and much of the brown leaf material and dead branches were evident on the trees and Juniper shrubs (personal observation).

In this article, I explore the idea that drought had a significant effect in restricting woody growth on the Burnt Lands Alvar through analysis of data on mortality of woody plants. In general, this work is designed to improve understanding of the derivation and future of alvar habitats by elucidating the factors that control species composition and, specifically, those that relate to the threat of forest encroachment.

Study Area

The Burnt Lands Alvar, 4 km northeast of Almonte, Mississippi Mills, Ontario, at approximately 45.2698, –76.1942 is a 15-km^2 area of provincially significant flora and fauna (Brunton 1986*), much of which is within Burnt Lands Provincial Park. The grasslands here are dominated by perennial Prairie Dropseed (*Sporobolus heterolepis* [A. Gray] A. Gray) and annual Sheathed Dropseed (*Sporobolus vaginiflorus* [Torrey ex. A. Gray]

FIGURE 1. Dead Common Juniper (*Juniperus communis*) in alvar grassland at the north end of the Burnt Lands Alvar, Eastern Ontario. The shrubs were killed by the extreme drought in 2012. Photo: P. M. Catling, September 2013.

Alph. Wood var. *vaginiflorus*) with numerous other prominent species characteristic of alvars also present, including Crawe's Sedge (*Carex crawei* Dewey), Small Skullcap (*Scutellaria parvula* Michaux), False Pennyroyal (*Trichostema brachiatum* L.), and Balsam Groundsel (*Packera paupercula* [Michaux Á. Löve & D. Löve). Other species locally common are Common Self-heal (*Prunella vulgaris* L.), Oxeye Daisy (*Leucanthemum vulgare* Lamarck), Tall Hawkweed (*Hieracium piloselloides* Vill.) and Common Viper's Bugloss (*Echium vulgare* L.). The grasslands are surrounded by forest dominated by Eastern White Cedar (*Thuja occidentalis* L.) with Common Juniper (*Juniperus communis* L.), White Pine (*Pinus strobus* L.), and White Spruce (*Picea glauca* [Moench] Voss). These woody species are also present as individuals within the grassland. The earlier established woody species provide shade that reduces water loss for later colonizers resulting in patches of woody plants. Through this process of nucleation, woodland begins to replace open alvar.

Methods

To test the hypothesis that the 2012 drought had a significant impact on woody species, the following data were gathered in late September 2013, one year after the drought and at a time when the drought impact was conspicuous with persisting dead branches and branches retaining brown leaves (Figures 1 and 2).

Age of woody vegetation killed

The age of some of the larger woody plants killed was determined by counting growth rings of cut dead trees with a stereo microscope. Resolution of growth rings was improved through the application of linseed oil to the cut surfaces. Seven Eastern White Cedars and three White Spruces were cut at breast height, and diameter at breast height (dbh) was measured. Five years was added to the growth ring estimates to account for the time required to reach breast height and make estimates of age more accurate. The ages of three White Pines were estimated by counting spaces between branches on the trunk. Three Common Junipers were cut at the stem base and growth rings were counted.

FIGURE 2. Dead Eastern White Cedar (*Thuja occidentalis*, front right) and dead White Spruce (*Picea glauca*, centre) in a nucleation patch with some living cedar (left) and half dead Common Juniper (*Juniperus communis*, bottom left). The dead cedar and spruce were approximately 30 years old as indicated by a count of growth rings. These trees were killed in 2012, when 60% of the trees in nucleation patches in the Burnt Lands Alvar, Eastern Ontario, died apparently due to extreme drought. Photo: P. M. Catling, September 2013.

Decline of woody vegetation along a limestone pavement crack

Based on the amount of living material compared with dead leaves and leafless branches, trees and shrubs were classified as dead, half dead, or alive and mapped along two, 25–m long cracks in the flat bedrock (limestone pavement) to provide a visual indication of the impact of the drought in an area of heavy damage. The area examined was rectangular (20 m × 25 m). Dbh for trees and maximum diameter of branch spread (i.e., of the patch) for juniper shrubs were recorded and indicated on the diagram (Figure 3). The dbh and shrub diameters were also used to calculate percentage decline (total dbh or patch size of dead material divided by total dbh or patch size times 100).

Juniper decline in open grassland

The maximum diameter of more or less circular patches of juniper was recorded in an open rectangular area 50 m × 100 m (5000 m^2) and the extent to which patches had died, in terms of percentage of lost surface area, was estimated to within 5%.

General decline of woody vegetation in open grassland

At three sites separated by 0.5–1 km, the status of all trees and shrubs in alvar grassland was recorded as dead, half dead, or alive (see above), and dbh for trees and maximum diameter for juniper shrubs was recorded. For each of the tree species and for each status category, the number of individuals, the dbh range and total of all dbh measurements were noted (Table 1). The sizes of areas surveyed are indicated in Table 1. From the data for dead tissue (total dbh for dead trees + ½ dbh for half dead trees), a percentage decline for all trees was calculated by dividing by the total dbh and multiplying by 100. A percentage decline for juniper shrubs was calculated by dividing loss of surface area by total surface area of patches times 100.

Documentation of the drought of 2012

Total rainfall for June, July, and August was used to identify drought years from 1890 to present. Rainfall is only an approximation of drought because the evenness of the pattern of rainfall for the period is not considered, nor is localized convectional rain, which may differ between a recording station and an area under consideration. The amount of heat, which increases water loss by evapotranspiration, is also an important factor that is not considered here. Although it is not an entirely reliable indication of drought, low total rainfall is highly correlated with severe drought impact and is, thus, helpful in determining drought occurrences if these limitations are taken into account.

Historical Environment Canada (2014) weather data for the closest stations were used. Because the record for the nearest town, Almonte, is incomplete, the record for Ottawa (45.38333, –75.71666), 40 km east by southeast of the study site, was used for the period 1890–2006. For 2007–2013, the potentially more accurate data from the nearby village of Appleton (45.18683, –76.10768), 12 km south by southeast of the study site, were used.

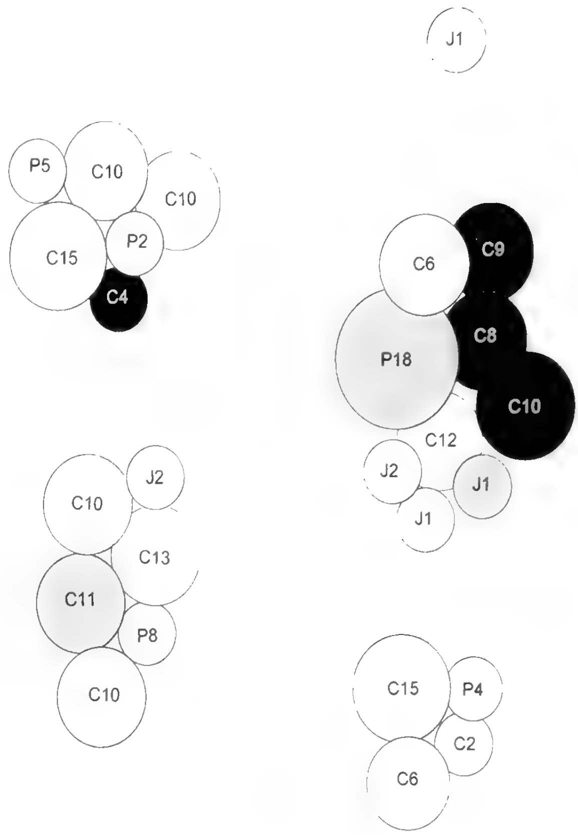

FIGURE 3. Diagram showing status of woody vegetation along two pavement cracks (stippled) at the north end of the Burnt Lands Alvar, Eastern Ontario. The diagram is based on a field sketch of a rectangular area 20 × 25 m and is drawn approximately to scale. Circles are trees and shrubs, where C = Eastern White Cedar (*Thuja occidentalis*), P = White Pine (*Pinus strobus*), J = Common Juniper (*Juniperus communis*) and white = dead, grey = half-dead, and black = alive. The numbers for cedar and pine are diameter of the trunk at breast height in cm; for junipers they are diameter of the whole shrub (m).

Results

Age of woody vegetation killed

The interpretation of growth rings was difficult in some areas and resulted in a range of values. Harvested Eastern White Cedar was 34–40 years old with dbh ranging from 15 to 17 cm. White Spruce was of similar age and diameter, while White Pine ranged from 35 to 50 years old. Most dead Common Juniper shrubs were older than the trees: 33–90 years old and 3–13 cm dbh.

TABLE 1. Measurements of dead, half dead and living Eastern White Cedar (*Thuja occidentalis*), White Spruce (*Picea glauca*), White Pine (*Pinus strobus*), and Common Juniper (*Juniperus communis*) at three open alvar grassland sites on the Burnt Lands Alvar, Eastern Ontario.

	Site 1 (45 × 80 m)			Site 2 (25 × 55 m)			Site 3 (28 × 42 m)		
Species and measures	Dead	Half dead	Alive	Dead	Half dead	Alive	Dead	Half dead	Alive
Eastern White Cedar									
Number	16	2	10	19	2	8	12	1	19
Dbh range (cm)	1–20	4	1–9.5	2–16	5–14	3–14	1–18	7	1.5–16
Total dbh (cm)	96.7	8	33.3	176	19	67	84	7	111
White Spruce									
Number	2	–	4		–	–	6		
Dbh range (cm)	5–6	–	3–12	–			2–10	–	
Total dbh (cm)	11	–	22	–	–	–	20		–
White Pine									
Number	2	–		–	–	2	3	1	
Dbh range (cm)	2.3–2.4	–	–	–	–	20–28	12–15	7	–
Total dbh (cm)	4.7	–	–	–	–	48	39	7	–
Common Juniper									
Number	8	1	5	1	3	3	1	3	1
Patch diameter (m)	0.8–2.5	0.6	0.3–1.8	2	3–5	2–4	1	1–3	4
Total of all patches (m)	10.9	0.6	3.9	2	12	9.5	1	5	4
All trees									
Total dbh (cm)	175.7			310.0			268.0		
% decline	66.3			59.8			56.0		
Common Juniper									
Total of all patches (m)	15.4			23.5			10.0		
% decline	72.7			34.0			35.0		

Decline of woody vegetation along a pavement crack

Most of the trees and shrubs in nucleation patches along a pavement crack were killed (Figure 3). The larger dead cedars (those about 15 cm dbh) in these patches were likely over 30 years old based on dbh of the few trees of definitely known age. The overall decline of trees in these pavement cracks was 80% and that of junipers was 93%.

Juniper decline in open grassland

Fifty-eight more-or-less circular patches of Common Juniper, 0.5–1 m in diameter occurred in the selected area. The majority of these shrubs were 35–45 years old based on basal stem diameters of a few trees of known age, and larger patches were composed of more than one plant. In 2012, 20 of the plants had died and many others had lost much of their foliage (Figure 1). The total area of living Common Juniper observed here at the start of 2012 had been approximately 274 m^2 and this had declined to 88 m^2 by the end of 2012, representing a 68% reduction. This area included shrubs up to 90 years old.

General decline of woody vegetation in open grassland

The overall decline of trees at three sites ranged from 56% to 66% and decline of junipers ranged from 35% to 73%. Thus over half of the woody vegetation in the openings was killed (Figure 2). Some of the trees at all three sites were over 35 years old, but all age classes and all three tree species were affected by the drought (Table 1).

Documentation of the drought of 2012

Since 1890, the average annual summer precipitation in the Ottawa area has been 255 mm. Based on this average and the pattern, a plot for this period (Figure 4) shows that unusually dry years (less than 160 mm of rain in June–August), approximately equivalent to the 2012 drought, have occurred on average

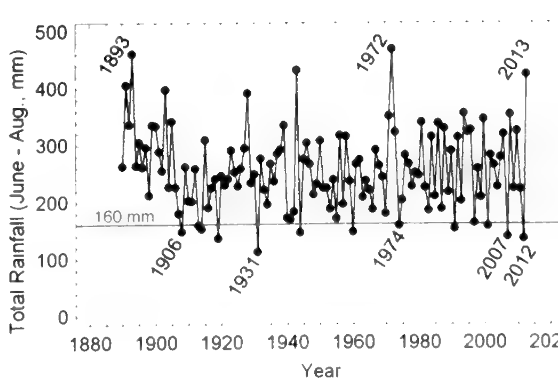

FIGURE 4. Summer rainfall (mm) from 1890 to 2013 near the Burnt Lands Alvar, Eastern Ontario, based on records of Environment Canada (2014).

every 8 years. The period from 1890 to 1906 was evidently the longest drought–free period on record. The 2012 drought was the second–most extreme in terms of limited rainfall (134 mm), the most extreme being the drought of 1931 (112 mm).

Unusually wet years (over 380 mm of rain in June–August) have occurred less frequently (Figure 4) than unusually dry years, with an average of 20 years between. Before 2013 (432 mm), the last unusually wet year occurred in 1972 (468 mm) and was the wettest on record.

Discussion

The 2012 drought had an impact on the Burnt Lands Alvar that was very similar to that reported for Maxton Plains (Stephenson and Herendeen 1986), where woody species mortality ranged from 10% to 100% at open alvar sites. The wide variation at Maxton Plains and Burnt Lands Alvar may have been based on differences in surface water flow, making some sites more susceptible to woody plant mortality than others.

The variation in the age of dead trees on Burnt Lands Alvar may be a consequence of random differences in times of establishment. Assuming that the same dry sites are susceptible to consecutive droughts, and based on the age range of 34–50 years of the larger dead trees, the last droughts as severe as that of 2012 occurred 52 years ago in 1960 and 38 years ago in 1974. However, some of the killed junipers were 87–90 years old and had survived droughts for almost 100 years. Although the wet years have allowed woody invasions, the higher frequency of dry years, some severe, has prevented encroachment of woody plants into grasslands and other open areas.

The drought of 2007 did not have as severe an impact on woody vegetation as that of 2012 (personal observation) despite similarly low overall rainfall (Figure 4). Possibly different rainfall patterns, less local rain, and higher heat contributed to the much greater severity in 2012. A drop to a critical level of dryness may also have played a role in 2012. Although not all dry periods indicated on the total rainfall diagram were severe enough to kill woody vegetation, those potentially capable of doing so have occurred with a high enough frequency that a drought averaging a 50% kill of woody vegetation in open alvar may have occurred once every 30 years over the past century. As this may be sufficient to maintain open alvar in many areas, it supports the conclusion of Stephenson and Herendeen (1986) that woody species encroachment into alvar grassland is not a threat to open alvar habitat. Studies of drought effects on some Scandinavian alvars, such as Stora Alvaret on the Swedish Island of Öland, have also documented a decline of juniper as a result of drought (Rosen 1984), although these alvars are often thought to have been largely created and maintained by livestock grazing (Znamenskiy *et al.* 2006).

By preventing encroachment of woody plants, periodic drought may provide a mechanism for the long-term persistence of species in alvars that are considered remnants of more continuous distributions in early postglacial landscapes. These occurrences of early postglacial and midwestern species assemblages, including, for example, the occurrence of the flightless leafhopper associated with the community–dominant Prairie Dropseed grass (Hamilton and Whitcomb 2010), now have a better supported theory to explain their isolation.

Although fire may have more impact on the edges of open alvar and in the creation of open alvar from alvar woodland (Catling 2009), or may vary in impact from one alvar to another (Jones and Reschke 2005), drought may prevent succession to forest on parts of open alvar and on alvar pavements not subject to fire. Drought may also promote fire by creating drier conditions and by increasing fuel. Consequently these processes may have a complementary effect in the maintenance of open conditions on alvars, but drought alone can have substantial impact.

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Received 6 January 2014
Accepted 14 February 2014

A Review of Colour Phenotypes of the Eastern Red-backed Salamander, *Plethodon cinereus*, in North America

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Moore, Jean-David, and Martin Ouellet. 2014. A review of colour phenotypes of the Eastern Red-backed Salamander, *Plethodon cinereus*, in North America. Canadian Field-Naturalist 128(3): 250–259.

The Eastern Red-backed Salamander (*Plethodon cinereus*) is the most abundant salamander species in many forests of northeastern North America. It is well-known for its colour polymorphism, which includes eight colour phenotypes: the red-backed (striped), lead-backed (unstriped) and erythristic morphs, as well as the iridistic, albino, leucistic, amelanistic and melanistic anomalies. Here we review the various colorations of *P. cinereus*, with the objective of facilitating the identification of these different phenotypes and of generating interest among field herpetologists and scientists reporting on this species. We also list six previously unpublished occurrences of colour variants in this species (1 case of erythrism, 3 of iridism, 1 of leucism, and 1 of partial leucism). To our knowledge, these cases include the first documented occurrence of iridism in the red-backed morph of *P. cinereus*, and the first two mentions of this colour anomaly in the lead-backed morph from Canada.

Key Words: Phenotypes; coloration; red-backed; lead-backed; erythristic; colour morph; iridistic; albino; leucistic; amelanistic; melanistic; colour anomaly; Eastern Red-backed Salamander; *Plethodon cinereus*; North America

Introduction

Of all North American amphibians, the Eastern Red-backed Salamander (*Plethodon cinereus*) is probably one of the most studied species, because of its wide distribution and abundance in forests of eastern Canada and northeastern United States (Highton 1962; Burton and Likens 1975; Petranka 1998), its ecological role (Burton and Likens 1975; Wyman 1998), and its potential as indicator of climatic change (Lotter and Scott 1977; Gibbs and Karraker 2006) and habitat disturbances (deMaynadier and Hunter 1995) in forest ecosystems. Striking colour polymorphism of this salamander species has long attracted the attention of scientists, herpetologists, and naturalists. Three pigment cell classes, or chromatophores, are responsible for skin coloration in amphibians (Bagnara 1966; Taylor and Bagnara 1972): melanophores (brown to black pigment cells), xanthophores (yellow and red (erythrophores) pigment cells), and iridophores, which produce the shiny iridescent and reflecting aspect of the amphibian skin.

In this article, we review the state of knowledge for each of the eight colour phenotypes known to date in *P. cinereus*, which include the red-backed (striped), lead-backed (unstriped) and erythristic morphs, as well as the iridistic, albino, leucistic, amelanistic and melanistic anomalies. Our objective is to provide a standardized description accompanied by photographs for the colour phenotypes reported for *P. cinereus*. Characteristics useful to discriminate among these different phenotypes are summarized. The North American distribution of the different colour morphs and anomalies in *P. cinereus* is also provided. Finally, we report six previously unpublished phenotype occurrences in this species (1 of erythrism, 3 of iridism, 1 of leucism, and 1 of partial leucism).

Colour Morphs

The red-backed and lead-backed colour morphs

The red-backed and lead-backed morphs (Figure 1) are the two most abundant phenotypes in *P. cinereus*. The ventral body of both morphs is coarsely mottled with black and white, resulting in a distinctive "salt-and-pepper" appearance (Figure 2; Table 1; Appendix). Individuals with intermediate colorations or other variations between these two morphs have been observed (e.g., Figure 3; Sipes 1964). The mid-dorsal stripe of the red-backed morph is generally red-orange, with gray-black borders that become mottled with white along the lower half of the body sides. Mid-dorsal stripe colours other than red-orange, such as shades of brown, gray, pink, white, and yellow have also been observed (e.g., Figures 4, 5; Bishop 1941; Test and Bingham 1948; Reed 1955; Schueler 1975; Hulse *et al.* 2001). Colour variations also include individuals with stripes that occur in disconnected sections along the body, and others with only continuous stripes on the tail (Bishop 1941; Cook 1967; Petranka 1998). The dorsum of the lead-backed morph does not exhibit stripes, and the coloration is generally a uniformly pigmented gray-black, but sometimes olive-gray or chestnut-brown (e.g., Figure 6; Klemens 1993). The dorsal-lateral body often exhibits some degree of iridescent or metallic, blue (Sawyers and Novick 2011), brassy, golden, shades of green or silver flecks (e.g., Figure 7).

Burger (1935) was the first to publish evidence that both morphs could be found in the same brood, which

TABLE 1. Main characteristics of the 8 colour phenotypes of the Eastern Red-backed Salamander (*Plethodon cinereus*).

Phenotype	Dorsal stripe	Dorsal-lateral body	Ventral body	Iris
Red-backed	Continuous or discontinuous red-orange stripe; sometimes shades of brown, gray, pink, white or yellow	Gray-black	"Salt-and-pepper" appearance	Normal (dark) pigmentation
Lead-backed	Unstriped	Gray-black; sometimes olive-gray or chestnut-brown	"Salt-and-pepper" appearance	Normal (dark) pigmentation
Erythristic	Unstriped	Red or orange, with or without black mottling	Red or orange	Normal (dark) pigmentation
Iridistic	Stripe present or absent	Generalized iridescent flecking (brassy, golden, shades of green or silver)	"Salt-and-pepper" appearance with or without iridescent flecking	Normal (dark) pigmentation
Albino	Unstriped	Pink-white to white	Pink-white to white, translucent	Red-pink
Leucistic	Unstriped	Pink-white to white	Pink-white to white, translucent	Normal (dark) pigmentation
Amelanistic	Peach-red, orange or peach-yellow	Pink-white to white	Pink-white to white, translucent	White to normal (dark) pigmentation
Melanistic	Unstriped	Black	Black, translucent	Brown to black

showed that they are of the same species (Highton 1959). Both morphs can be found across the species range, throughout southeastern Canada and the eastern United States (Petranka 1998), but in very different proportions (Moore and Ouellet 2014). In some areas, both morphs are abundant, while in others, one or the other is more abundant. Monomorphic red-backed populations are not uncommon, while in other cases, red-backed individuals can be scarce or absent (Thurow 1955; Highton 1959; Pfingsten and Walker 1978; Reichenbach 1981; Fisher-Reid *et al.* 2013). The red-backed morph has been reported in five Canadian provinces and 22 American states (Table 2), which represents the distribution range of this species. Kentucky, Minnesota, and Tennessee are at the limit of the species' range and the lead-backed morph of *P. cinereus* has not been reported there.

In the last decades, studies have suggested that the lead-backed morph of *P. cinereus* is more closely associated with warmer climates than the red-backed morph (Lotter and Scott 1977; Moreno 1989; Gibbs and Karraker 2006; Anthony *et al.* 2008). However, it seems that the possible role of climate in the distribution of the lead-backed morph has never been unanimously recognized; some doubts still persist in the scientific community about the validity of using this morph as indicator of climatic changes (Angleberger and Chinnici 1975; Pfingsten and Walker 1978; Petruzzi *et al.* 2006; Anthony *et al.* 2008). Based on new discoveries in the northern areas of the species' range and on the largest compilation ever made for this species. Moore and Ouellet (2014) demonstrate however that climate and geographic variables do not influence the colour morph proportions in *P. cinereus* populations. Fitzpatrick *et al.* (2009) mentioned that the most reasonable hypothesis to explain the existence of visual polymorphism across a geographical and phylogenetic range as wide as that of *P. cinereus* is that selection acts directly on appearance. Local natural selection could explain the morph frequency in given areas.

The erythristic colour morph

Erythrism (from Greek *eruthros*, red) refers to an excessive production and deposition of red or orange pigments (erythrophores). The erythristic morph of *P. cinereus* (Figures 8, 9) is usually all red or orange, but may exhibit varying degrees of black mottling on its dorsal and lateral surfaces. The ventral surface is generally red, orange or pink (Reed 1955; Thurow 1961; Rosen 1971). Some intermediate colorations (partial erythrism) also exist (e.g., Figure 10). The erythristic morph has been found in four provinces (Brown 1928; Bleakney and Cook 1957; Cook and Bleakney 1961) and 10 states (Reed 1908; Reed and Wright 1909; Barbour 1914; Burt 1945; Matthews 1952; Pfingsten 1969; Mueller and Himchak 1983; deMaynadier 1995; McDonald *et al.* 2011), but it is more frequently found in United States than in Canada. The prevalence of this morph in the United States can sometimes be as high as 35-50% (Pauley *et al.* 2001; Cassell and Jones 2005), but generally rarely exceeds 20% (Lotter and Scott 1977; Tilley *et al.* 1982). According to Pauley *et al.* (2001), the distribution of this morph would be limited to cooler climates of glaciated areas of southern Canada and the northeastern United States. In this context, the apparent rarity of the erythristic morph in eastern Canada remains enigmatic. Thirty-seven erythristic

FIGURE 1. Red-backed (striped) and lead-backed (unstriped) morphs of the Eastern Red-backed Salamander (*Plethodon cinereus*) from Québec. Photo: M. Ouellet.

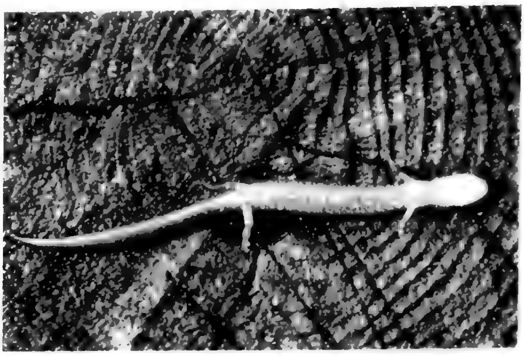

FIGURE 2. Distinctive "salt-and-pepper" appearance of the ventral body of a lead-backed morph of *P. cinereus* from Québec. Photo: M. Ouellet.

FIGURE 3. Slight colour variation of a red-backed morph of *P. cinereus* from Québec. Photo: M. Ouellet.

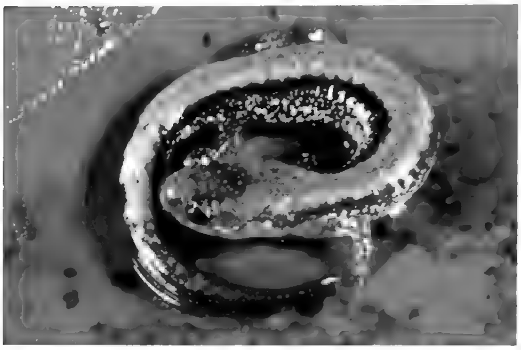

FIGURE 4. Cream coloration of the dorsal stripe of a red-backed morph of *P. cinereus* from New Hampshire. Photo: D. J. Hocking.

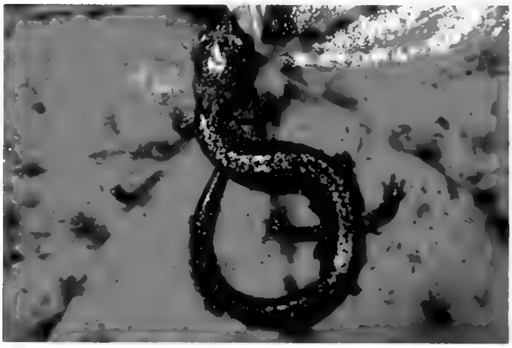

FIGURE 5. Shade of gray coloration of the dorsal stripe of a red-backed morph of *P. cinereus* from Ohio. Photo: C. D. Anthony.

FIGURE 6. Chestnut coloration of a lead-backed morph of *P. cinereus* from Québec. Photo: M. Ouellet.

FIGURE 7. A lead-backed morph of *P. cinereus* with blue iridophores from Maine. Photo: D. E. Swann.

FIGURE 8. An erythristic morph of *P. cinereus* from Québec. Photo: P. Beaupré.

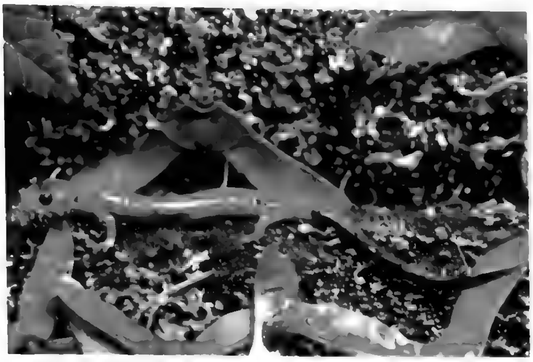

FIGURE 9. Another example of erythrism of *P. cinereus*, with black mottling on the tail, from Nova Scotia. Photo: R. Merrick.

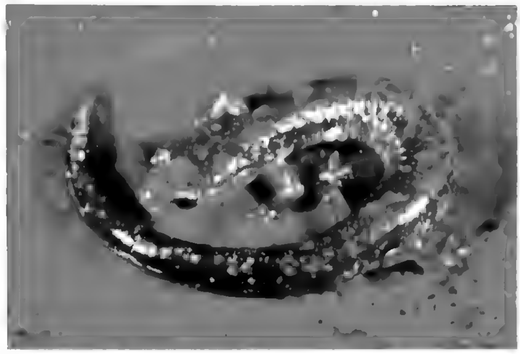

FIGURE 10. A partially erythristic morph of *P. cinereus* from New Hampshire. Photo: D. J. Hocking.

FIGURE 11. An iridistic colour anomaly of a red-backed morph of *P. cinereus* from North Carolina. Photo: L. A. Williams.

FIGURE 12. Iridism of a lead-backed morph of *P. cinereus* from Nova Scotia. Photo: J. Gilhen.

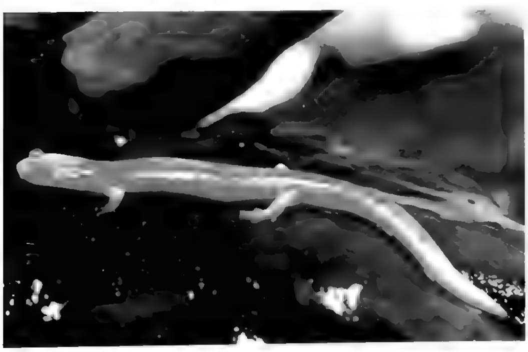

FIGURE 13. An albino colour anomaly of *P. cinereus* from Nova Scotia. Photo: J. Gilhen.

FIGURE 14. A leucistic colour anomaly of *P. cinereus* from Québec. Photo: I. Bouthillier.

FIGURE 15. Another example of leucism of *P. cinereus* from Nova Scotia. Photo: J. Gilhen.

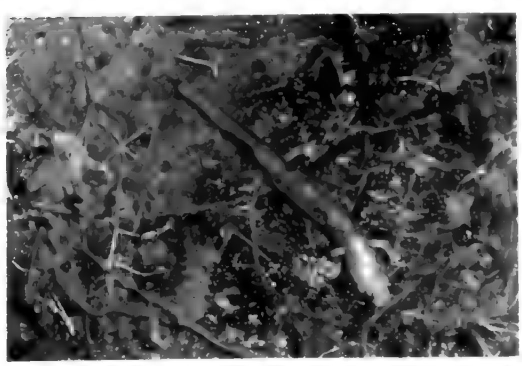

FIGURE 16. Dorsal view of a partially leucistic *P. cinereus* from Québec. Photo: P. Beaupré.

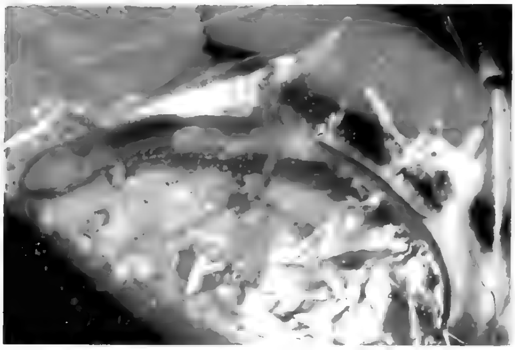

FIGURE 17. Ventral view of the previous specimen of a partially leucistic *P. cinereus*, showing the translucent aspect of the body. Photo: P. Beaupré.

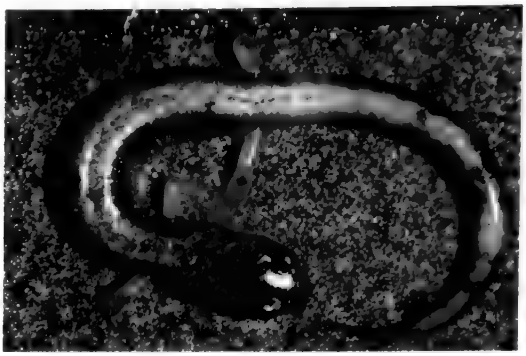

FIGURE 18. A partially leucistic *P. cinereus* from Ohio. Photo: C. D. Anthony.

FIGURE 19. An amelanistic colour anomaly of *P. cinereus* from Québec. Photo: J.-D. Moore.

FIGURE 20. Another example of amelanism of *P. cinereus* from Ohio (the red-eye effect is due to the photographic flash). Photo: J. G. Davis.

individuals have been reported in Canada (e.g., Piersol 1909; Gilhen 1968; Rosen 1971; Westell and Ross 1974; Jongsma 2012a), including a new occurrence for Québec (Figure 8). This specimen was observed in October 2005 in the La Haute-Yamaska Regional County Municipality, Québec (45°21'20"N, 72°37'18"W; datum = NAD83). Jongsma (2012a) reported 11 erythristic individuals among 85 *P. cinereus* specimens in Fredericton, New Brunswick, thus demonstrating that some salamander populations in eastern Canada could nevertheless show a high prevalence of erythrism.

Thurow (1955) mentioned that the nature of the erythristic form and its distribution suggest that genetic rather than environmental factors are involved. According to his interpretation, this phenotype could result from the action of a mutant allele that quantitatively inhibits the development of melanin (or possibly melanophores). For intermediate colorations of this morph, the author noted the possibility of only partial dominance or the involvement of more than one locus. Other studies suggested that erythristic *P. cinereus* may be the Batesian mimic of the Eastern Newt (*Notophthalmus viridescens*) at the eft stage (Lotter and Scott 1977; Tilley *et al.* 1982; Cassell and Jones 2005), which is known to be toxic for potential predators (Brodie *et al.* 1974). This phenomenon would partly explain the high abundance of the erythristic morph in some forests where the red eft is present. However, the presence of the red eft in northern forests does not necessarily imply that the erythristic morph will be found in these ecosystems (Moore *et al.* 2012).

Colour Anomalies

The iridistic colour anomaly

Iridism in amphibians is defined as the excessive production and deposition of iridophore platelets. Individuals are characterized by generalized iridescent or metallic, brassy, golden, shades of green or silver flecks on their dorsal-lateral body. This condition has previously been described (Muchmore 1955; Hertzler 1958) and reported for the lead-backed morph of *P. cinereus* in the United States (Bogert 1952; Highton 1962, 1972; Schueler 1975; Klemens 1993; Hulse *et al.* 2001; Gibbs *et al.* 2007). However, it was not always clear from these documents whether the iridescent flecking was very abundant or visible only upon close examination. Muchmore (1955) noted that microscopic examination revealed that this flecking was due to numerous individual iridophores located around the melanophores. These flecks are also known to fade rapidly on preserved specimens (Grobman 1949; Muchmore 1955; Pfingsten and Downs 1989).

We report here three previously unpublished occurrences of iridistic *P. cinereus*, including, to our knowledge, the first documented occurrence of iridism in the red-backed morph and the first two mentions in lead-backed morphs from Canada. In all these cases, the dorsal body exhibited abundant, continuous, and

TABLE 2. North American distribution of the 8 different colour morphs and anomalies of the Eastern Red-backed Salamander (*Plethodon cinereus*). Abbreviations: Red = red-backed morph, Lea = lead-backed morph, Ery = erythristic morph, Iri = iridistic anomaly, Alb = albino anomaly, Leu = leucistic anomaly, Ame = amelanistic anomaly, Mel = melanistic anomaly.

Province or State	Red	Lea	Ery	Iri	Alb	Leu	Ame	Mel
Connecticut	■	■	■					
Delaware	■	■						
Illinois	■	■						
Indiana	■	■						
Kentucky	■							
Maine	■	■	■		■			
Maryland	■	■	■		■	■		
Massachusetts	■	■	■	■		■		
Michigan	■	■		■				
Minnesota	■							
New Brunswick	■	■	■		■			
New Hampshire	■	■	■					
New Jersey	■	■		■				
New York	■	■	■	■		■		
North Carolina	■	■		■				
Nova Scotia	■	■	■	■	■	■	■	
Ohio	■	■	■	■		■	■	
Ontario	■	■	■		■	■		
Pennsylvania	■	■	■	■				
Prince Edward Island	■	■						
Québec	■	■	■	■		■	■	■
Rhode Island	■	■	■					
Tennessee	■							
Vermont	■	■	■					
Virginia	■	■		■				
West Virginia	■	■		■		■		
Wisconsin	■	■						

large iridescent brassy flecks. The first individual (Figure 11) was observed in September 2012 in Ashe County, North Carolina (36°25'35"N, 81°35'26"W; datum = WGS84), and the second (Figure 12) was reported in June 1982 in Colchester County, Nova Scotia (45°23'37"N, 63°55'04"W; datum = NAD83). The third specimen was observed in October 2013 in the Antoine-Labelle Regional County Municipality, Québec (46°43'03"N, 75°33'06"W; datum = NAD83). These occurrences show that iridescent flecking is sometimes quite abundant and may represent the dominant colour in some *P. cinereus* individuals. Added with cases from other studies (e.g., Muchmore 1955), they also suggest that iridism in *P. cinereus* is probably more common than previously reported, and thus deserves to be regarded as a noteworthy colour variant. To date, it has been reported in two provinces and 9 states (Table 2).

The albino colour anomaly

Albinism (from Latin *albus*, white) is defined as the total absence of pigmentation formation in the skin and irises. The albino *P. cinereus* is unstriped and characterized by a flesh-colored body (pink-white to white) and red-pink irises (Figure 13). According to the literature, this anomaly has been observed three times in Canada (Milnes 1946; Moore *et al.* 2012) and three times in the United States (Fowler 1942; Hensley 1959; Harris 1968a), though no detailed description of the specimens was given by Milnes (1946) nor Harris (1968a). The only case mentioned in Québec (Moore *et al.* 2012) has been redefined as an amelanistic *P. cinereus*, after the photographic verification showed normal (dark) pigmentation of the irises, a light orange dorsal stripe and the pink-white colour of the specimen's dorsal-lateral body. Similarly, the albino case reported by Harris (1968b) was redefined as an amelanistic, based on a published photograph (Zahl 1972).

The leucistic colour anomaly

Leucism (from Greek *leukos*, white) is a defect in the skin causing an inability to support any type of skin pigments. Since all types of skin pigments are thus reduced, leucistic individuals resemble albino *P. cinereus* (Figures 14, 15), except for their normally pigmented irises. This explains why this condition has also been defined in the past as "albinos with orbital melanophores" (Brame 1962), or "partial albinos" (Gilhen 1986). The leucistic anomaly has been observed four times in Canada (Gilhen 1986 (based on the colour photo NSM973-634-1); Rye 1991; Lamond 1994; Jongsma 2012b) and six times in the United States (Wilmott

1945; Pauley 1974; Lotter and Scott 1977 (white partial albino); Mitchell and Mazur 1998; Mendyk *et al.* 2010). A previously unpublished occurrence of leucism (Figure 14) was observed in September 2013 in the Thérèse-De Blainville Regional County Municipality, Québec (45°39'28"N, 73°54'33"W; datum = NAD83). An unpublished occurrence of partial leucism (Figures 16, 17) was also reported in September 2005 in the Nouvelle-Beauce Regional County Municipality, Québec (46°32'30"N, 71°00'01"W; datum = NAD83). Leucism was considered as partial in this specimen, due to the presence of melanophores. Two similar cases have also been described in Ohio (Figure 18, Paluh *et al.* 2013).

The amelanistic colour anomaly

Amelanism is a condition characterized by the lack of melanin production. The appearance of this anomaly on the skin depends on the remaining non-melanin pigments. Although similar, amelanistic *P. cinereus* salamanders may retain more coloration than the albino and leucistic anomalies, and are characterized by a body without black pigmentation (Figures 19, 20). The dorsal stripe is typically pale in colour, usually peach-red, orange or peach-yellow. The dorsal-lateral body is often pink-white to white, the ventral body is sometimes translucent, and the iris colour may vary from white to normal (dark).

This colour anomaly has been reported five times in eastern Canada (Gilhen 1986 (based on the colour photo NSM984-108-1); Moore and Gilhen 2011; Russell *et al.* 2011; see also the above section on the albino anomaly), and twice in the United States (Davis 2009; see also the above section on the albino anomaly). Some authors may sometimes have considered the amelanistic condition as partial albinism, using terminology such as "albinos with xanthophores" or "partial albino with xanthophores" and "albinos with erythrophores" or "partial albino with erythrophores" (Brame 1962; Harris 1970; Dyrkacz 1981).

The melanistic colour anomaly

Melanism (from Greek *melas*, black) is a condition characterized by an overabundance of melanin pigments (melanophores) production and deposition. Melanistic individuals are usually totally black, including the ventral body and irises. This condition is somewhat the opposite of amelanism. This anomaly in a *P. cinereus* was first mentioned in Québec (Moore *et al.* 2012). With its uniformly black and translucent belly, the melanistic individual is relatively easy to distinguish from the lead-backed morph (occasionally very dark), which has a salt-and-pepper belly appearance. The melanistic anomaly is not new and has already been encountered in other salamander and anuran species, in which the ventral body is sometimes translucent (Dubois, 1979).

Conclusion

Eight colour phenotypes of the woodland salamander *P. cinereus* have been reported to date. These include main colour morphs as well as rarer colour anomalies. To discriminate among these different phenotypes, useful characteristics are summarized in Table 1, and a dichotomous key is provided (Appendix). Contrary to amphibian malformations that are mostly found in young individuals and rarely in adults because they are maladaptive (Ouellet 2000), most of the *P. cinereus* specimens encountered that exhibit colour anomalies are adults. We agree with Mendyck *et al.* (2010) that these colour conditions may be less detrimental for this secretive species than for other amphibians, and thus more likely to be present.

We hope that this article and the greater accessibility of digital photography will encourage documenting these atypical cases in future inventories. We suggest using uniform colour names based on an easily-accessible online list of colours (Wikipedia 2014). This list is preferred over other guides (e.g., Smithe 1975) which are rather more difficult to obtain. An ongoing colour photo gallery is currently online for recognition and comparison purposes (http://www.amphibia-nature.org/en/projects/amphibians-reptiles/colorations-plethodon/). Photos of unusual colorations with the date, location, and details about the observation can be sent to the following address: info@amphibia-nature.org. Close-up pictures that show the colour of the dorsal stripe, dorsal-lateral body, ventral body, and irises are preferred.

Acknowledgements

We are grateful to all photographers who kindly contributed pictures of *P. cinereus* to illustrate this article: C. D. Anthony (John Carroll University); P. Beaupré (Ministère du Développement durable, de l'Environnement, de la Faune et des Parcs du Québec); L. Bouthillier (Ministère du Développement durable, de l'Environnement, de la Faune et des Parcs du Québec); J. G. Davis (Cincinnati Museum Center); J. Gilhen (Nova Scotia Museum of Natural History); D. J. Hocking (University of New Hampshire); R. Merrick; D. E. Swann; and L. A. Williams (North Carolina Wildlife Resources Commission). We also acknowledge C. Genest (Amphibia-Nature) for sharing her field observations, P. Galois (Amphibia-Nature) and D. Tousignant (Forêt Québec) for reviewing an earlier version of this manuscript, J. G. Davis for some museum data contribution, and J. T. Bagnara (Professor Emeritus, University of Arizona), F. R. Cook (Canadian Museum of Nature), J. Gilhen, T. B. Persons (USGS Southwest Biological Science Center) and F. W. Schueler (Bishops Mills Natural History Centre) for helpful comments.

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Received 27 March 2014
Accepted 24 April 2014

Appendix

Dichotomous key of the 8 different colour phenotypes of the Eastern Red-backed Salamander (*Plethodon cinereus*).

1.a Presence of a continuous or discontinuous dorsal stripe: 2
1.b Absence of a dorsal stripe: 4
2.a Presence of melanophores on the skin surface: 3
2.b Absence of melanophores, dorsal-lateral body pink-white to white: **Amelanistic anomaly** (Figures 19, 20)
3.a Generalized iridescent flecking: **Iridistic anomaly** (Figure 11)
3.b No generalized iridescent flecking: **Red-backed morph** (Figures 1-5)
4.a Presence of melanophores on the skin surface: 5
4.b Absence of skin melanophores: 8
5.a Presence of red or orange pigmentation: **Erythristic morph** (Figures 8-10)
5.b Absence of red pigmentation: 6
6.a "Salt-and-pepper" appearance of the ventral body: 7
6.b Black and translucent ventral body: **Melanistic anomaly**
7.a Generalized iridescent flecking: **Iridistic anomaly** (Figure 12)
7.b No generalized iridescent flecking: **Lead-backed morph** (Figures 1, 2, 6, 7)
8.a Red-pink pigmentation of the irises: **Albino anomaly** (Figure 13)
8.b Normal (dark) pigmentation of the irises: **Leucistic anomaly** (Figures 14-18)

Notes

Long-distance Anadromous Migration in a Fresh Water Specialist: the Lake Trout (*Salvelinus namaycush*)

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Harris, Les N., Jean-Sébastien Moore, Christopher G. McDermid, and Heidi K. Swanson. 2014. Long-distance anadromous migration in a fresh water specialist: the Lake Trout (*Salvelinus namaycush*). Canadian Field-Naturalist 128(3): 260–264.

The Lake Trout, *Salvelinus namaycush*, is believed to be one of the most saline intolerant salmonid species, typically completing its life wholly in fresh water. Historical observations and more recent quantitative assessments have shown, however, that in some Arctic populations, Lake Trout can migrate to marine waters (i.e., display anadromy). In the four coastal Arctic populations of Lake Trout where anadromy has been confirmed, migrations to and from marine environments are relatively short (i.e., in the order of a few kilometres). In the Halokvik River on Victoria Island, we captured two anadromous Lake Trout in a weir used jointly for commercial fishing and stock assessment research. Both fish were captured during the fall upstream migration, some 50 km from their presumed fresh water spawning or overwintering locations. This observation extends the current knowledge regarding the distribution of anadromous populations in this species and suggests that migration to marine habitats can be much longer than previously expected.

Key Words: Lake Trout; *Salvelinus namaycush*; anadromy; migration; Victoria Island

Introduction

Migration is a coordinated movement that is evolutionarily advantageous because of the fitness benefits associated with movement to an alternate habitat (Hendry *et al.* 2004; Binder *et al.* 2011). Fishes in particular are well known for extraordinary migrations that can be classified based on the aquatic biomes through which they move. Diadromy is a type of migration in which the marine–fresh water boundary is crossed (Binder *et al.* 2011), and anadromy is a unique type of diadromy, in which fishes hatched in fresh water subsequently migrate to marine habitats for feeding and, eventually, undertake a return migration to fresh water for spawning, overwintering, or both (McDowall 1997, 2007). This life history strategy is exemplified in the salmonid fishes and is typically more prevalent at higher latitudes (Gross *et al.* 1988; McDowall 2008). Anadromous migrations within this group can be quite remarkable, ranging from thousands of kilometres (Stephenson *et al.* 2005) to just hundreds of metres (Harris *et al. in press*).

Among salmonids, Lake Trout (*Salvelinus namaycush*) are generally thought to be the least tolerant of saltwater conditions (Quinn 2005). Lake Trout were typically believed to be invariably non-anadromous (Hendry *et al.* 2004), but were recently shown to be able to survive salinities equal to that of full-strength sea water (i.e., 30%, Hiroi and McCormick 2007). Lake Trout have been observed sporadically, although rarely, in marine waters (dating back to the 1950s and reviewed in Martin and Olver 1980), and recent data from otolith microchemistry and stable isotope analyses confirm that some coastal Canadian Arctic populations of Lake Trout do make annual migrations to marine environments (Swanson *et al.* 2010). Among four study populations, 27% of Lake Trout made annual migrations to the sea, and anadromous Lake Trout were in better condition and had lower concentrations of mercury than fresh water resident Lake Trout (Swanson and Kidd 2009; Swanson *et al.* 2010). Further study using isotope mixing models found that marine prey items constituted a large proportion (66%) of the diet of anadromous Lake Trout (Swanson *et al.* 2011).

Despite this recent increase in our knowledge of anadromy in the Lake Trout, much remains unknown regarding the distribution of its life history across the northern range of the species and the magnitude of the migrations it undertakes. Where anadromy has been confirmed in Lake Trout, migration distances have been relatively short (< 3 km, Swanson *et al.* 2010), suggesting that Lake Trout employing this life history tactic are associated with systems in which the distance to marine waters is short. Here, we describe a case of long-distance migration in anadromous Lake Trout based on observational evidence and capture data accumulated

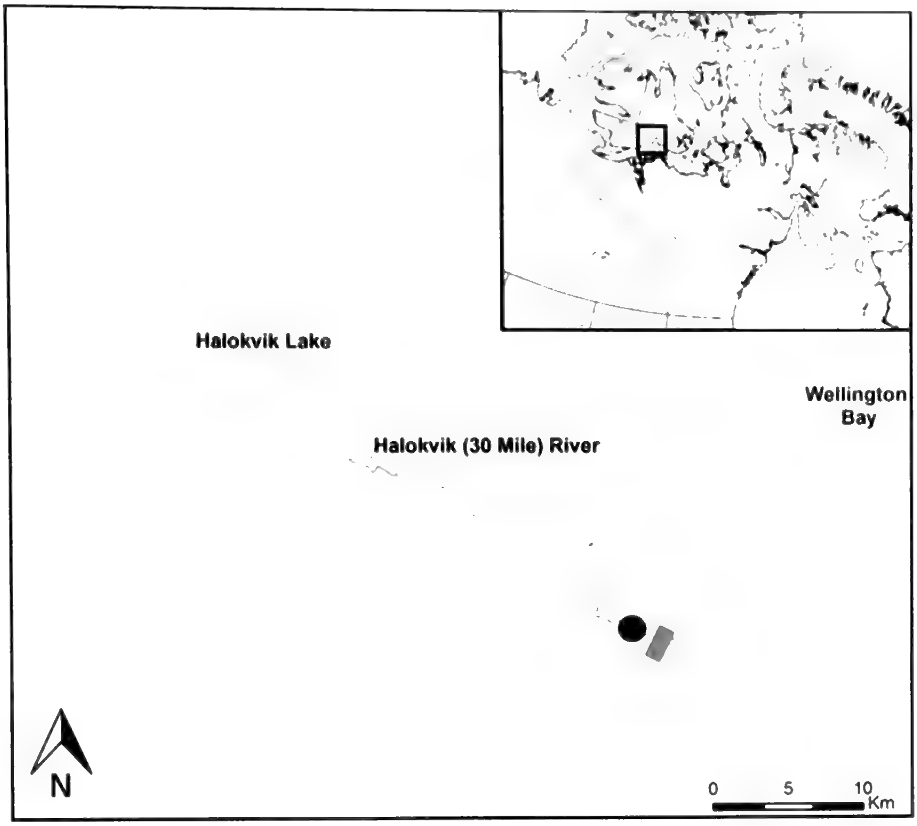

FIGURE 1. Map of the study area showing the location of the Halokvik River (30 Mile) on Victoria Island, Nunavut. Also shown is the location of the weir constructed in 2013 (red rectangle), the position of the acoustic receiver deployed in the river (black circle), and Halokvik Lake where anadromous Lake Trout (*Salvelinus namaycush*) are presumed to overwinter, some 50 km from the weir.

from a fisheries weir assessment on the Halokvik River (locally known as 30 Mile), Victoria Island. This river is located in the Canadian Arctic (Figure 1), approximately 80 km west of the community of Cambridge Bay in Nunavut.

Methods and Observations

In 2013, Fisheries and Oceans Canada operated a conduit weir on the Halokvik River with the intention of enumerating anadromous Arctic Char (*Salvelinus alpinus*) migrating upstream. The Halokvik River drains a large system of lakes that flow into the west side of Wellington Bay. The last lake draining into this river, locally known as Halokvik Lake, is located some 50 km upstream from the ocean and is presumed to be the furthest downstream lake capable of supporting Arctic Char and Lake Trout (J. Hiniliak, Cambridge Bay elder, personal communication, 2013).

The weir, which spanned the entire river (Figure 2) to ensure that all upstream-migrating fish were captured, was designed following the methods outlined by McGowan (1990). It was located near the river mouth, 50 m from tidal-influenced brackish waters. The weir was operated continually from August 8 to September 10, 2013. In mid-August 2013 (August 16 and 18), two Lake Trout (Figure 3) were captured in the weir as they were most certainly migrating back into fresh water to spawn and/or overwinter, presumably in habitats located 50 km upstream. Lake Trout 1 was 576 mm in fork length and weighed 2100 g and Lake Trout 2 was 531 mm in length and weighed 1700 g. Both fish were photographed for morphometric analyses, tissue samples were obtained, and the opportunity was taken to implant both with acoustic transmitters (V16 Coded Acoustic Transmitters, VEMCO, Bedford, Nova Scotia).

Discussion

Although the Lake Trout is often believed to be restricted to fresh water for its entire life cycle, evidence that anadromy may be common in high latitude populations is accumulating. Populations in which anadromy has previously been documented, however, have been found at very short distances from the marine environment (within 3 km, Swanson *et al.* 2010). Here, we report the capture of two Lake Trout returning from marine waters some 50 km downstream from the closest lake where overwintering and/or spawning would be possible. It is highly unlikely that these two fish were riverine Lake Trout, given that the Halokvik River freezes solid during winter over most of its course. Furthermore, they were captured in a weir approxi-

FIGURE 2. Aerial view of the weir across the Halokvik River, Victoria Island, Nunavut, used in 2013 as part of an Arctic Char (*Salvelinus alpinus*) population assessment. The red arrow indicates the upstream direction of migration. Photo courtesy of Denise LeBleu Images.

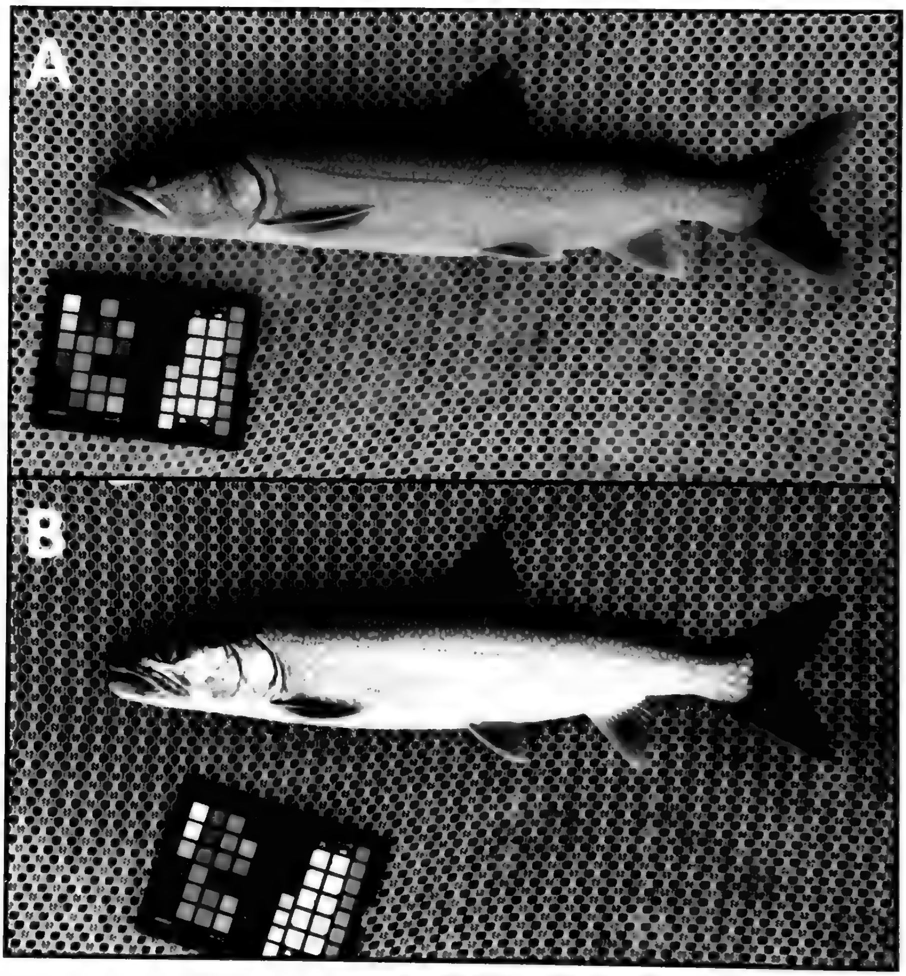

FIGURE 3. The two Lake Trout (*Salvelinus namaycush*) captured in the Halokvik (30 Mile) River weir, Victoria Island, Nunavut, while migrating from marine waters to spawning and overwintering locations located 50 km upstream. (A) Lake Trout 1; (B) Lake Trout 2.

mately 50 m from tidal influenced waters and, given the energy costs of migration, it is highly unlikely that Lake Trout would migrate 50 km to exploit fresh water river habitat, which is much less productive than the adjacent brackish and marine habitats. Thus, to our knowledge, this represents the longest documented anadromous migration of Lake Trout, highlighting an unappreciated ability for long-distance migration to and from marine environments in a species that was once thought to be restricted to fresh water.

Local knowledge in the Cambridge Bay region indicates that Lake Trout are sometimes caught in marine waters (B. Nakashook, Cambridge Bay resident, personal communication, 2013). Recently, quantitative evidence of anadromy in Arctic populations of Lake Trout has become available to corroborate this local knowledge (Swanson *et al.* 2010) and, combined, these pieces of information indicate that anadromy in this species may not be as rare as once assumed. For instance, in Nauyuk Lake, a system located on the mainland of Canada approximately 90 km southwest of the Halokvik River, 40% of assessed Lake Trout were classified as anadromous (Swanson *et al.* 2010). However, marked variation occurred in the proportion of resident versus anadromous fish in other proximate systems (Swanson *et al.* 2010) and, currently, no fully anadromous populations are known. Further work is thus required to truly understand intra- and inter-population variation in anadromy in this species and to resolve the specific mechanisms responsible for driving such differences.

Information on the population and biological parameters of anadromous Lake Trout are virtually absent (but see Swanson *et al.* 2010, 2011). Little is known regarding sizes and ages of anadromous individuals, however, among the four systems located across Dease Strait that were studied by Swanson *et al.* (2010), age of first migration in Lake Trout varied widely: from 3 to 29 years of age (mean, 13 years). Lake Trout started migrating to sea at a significantly older age on average than sympatric anadromous Arctic Char (5 years of age), and at 13 years of age, first-year migrant Lake Trout were larger (mean 400 mm fork length) than first-year migrant Arctic Char (mean 275 mm, Swanson *et al.* 2010). The anadromous Lake Trout observed in this assessment are within the length ranges reported by Swanson *et al.* (2010).

Little information is available on the distribution of anadromy in Lake Trout, and further work is required to quantify the prevalence of this life history tactic throughout the northern range of the species. There are, however, reports of anadromous Lake Trout on other Canadian Arctic islands (Manning 1953), and work is ongoing to provide the first assessment on the distribution of anadromy in this species across the coastal Canadian Arctic. Finally, marine habitats used by anadromous Lake Trout are not well characterized. As with other salmonids, they likely prefer brackish coastal waters for feeding on marine invertebrates and fishes (Swanson *et al.* 2011). Acoustic receivers are currently positioned in the brackish and marine habitats near the mouth of the Halokvik River, and future acoustic telemetry readings may provide the first data on marine habitat use by this species.

Given the considerable distance presumably covered by Lake Trout in our study, marine migrations are not likely opportunistic forays, but rather concerted efforts to access marine habitats. High energetic costs of migration and the potential increased risk of predation (Hendry *et al.* 2004) mean that the fitness benefits of migrating to marine habitats must be substantial and must outweigh the fitness benefits of remaining in fresh water (Gross 1987). Indeed, oceans are much more productive than fresh water in north-temperate and Arctic environments, and the prevalence of anadromy appears to increase at higher latitudes (McDowall 1987; Gross *et al.* 1988). Thus, it is likely that anadromous Lake Trout observed in the Halokvik River were accessing marine habitats to take advantage of rich food sources and that this results in higher growth rates, larger size-at age, and greater energy stores (Hendry *et al.* 2004). This in turn, may result in higher fecundity and overall fitness compared with their fresh water counterparts (Roff 1988). Swanson *et al.* (2010) found that the diet of anadromous Lake Trout was composed of about 66% marine-derived prey (based on stable isotope mixing models) and that anadromous Lake Trout were typically in better condition than their fresh water counterparts. This is consistent with the hypothesis that anadromous Lake Trout are migrating to exploit relatively rich marine food sources.

In conclusion, our observations provide novel insight into the distribution of anadromy in Lake Trout populations in the Arctic, now confirming it on Victoria Island, and highlight the potential for long-distance migration in this species as a tactic in a life history that has remained relatively enigmatic.

Acknowledgements

We thank the Ekalluktutiak Hunters' and Trappers' Organization for help with logistic planning over the course of the field season. Jack (Meyok) Omilgoetok worked on all aspects of the field work and was instrumental in the success of our field season. Jimmy Haniliak helped with tagging at the Halokvik River and Johnny Pedersen assisted with weir construction. We also thank Jimmy Haniliak and Brent Nakashook for providing information on the Halokvik River system. Funding for this project was provided by Fisheries and Oceans Canada (through Nunavut Implementation Funds) and the Nunavut Wildlife Management Board.

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Received 7 February 2014
Accepted 31 March 2014

New Records of the Ogilvie Mountains Collared Lemming (*Dicrostonyx nunatakensis*) in central Yukon

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Jung, Thomas S., Brian G. Slough, David W. Nagorsen, and Piia M. Kukka. 2014. New records of the Ogilvie Mountains Collared Lemming (*Dicrostonyx nunatakensis*) in central Yukon. Canadian Field-Naturalist 128(3): 265–268.

The Ogilvie Mountain Collared Lemming (*Dicrostonyx nunatakensis* Youngman, 1967), reported only from the Ogilvie Mountains of central Yukon, is among the least known mammals in Canada. It was first discovered in 1961 and, since then, only 13 specimens had been collected, all from one mountain, in central Yukon. We conducted a targeted survey to determine the distribution of the species by trapping areas of apparently suitable habitat on 12 mountains within 40 km of the known location. Many of our traps were disabled by other mammals; however, we captured three Ogilvie Mountain Collared Lemmings on two mountains 25.9 km and 29.6 km from the original location. Our findings suggest that this lemming may be more widely distributed than indicated by earlier specimens. We suggest further surveys to delineate the range of the Ogilvie Mountain Collared Lemming.

Key Words: Ogilvie Mountain Collared Lemming; *Dicrostonyx nunatakensis*; distribution; Tombstone Territorial Park; Yukon

Introduction

The Ogilvie Mountain Collared Lemming (*Dicrostonyx nunatakensis* Youngman, 1967) is known from only one mountain in central Yukon, Canada. Collared Lemmings in the Ogilvie Mountains are geographically separated from populations of Nearctic Collared Lemming (*Dicrostonyx groenlandicus*) to the northeast by about 250 km of apparently unoccupied habitat. The nearest recorded population of Nearctic Collared Lemming is in the Richardson Mountains, northeast of the Ogilvie Mountains. Youngman (1967) speculated that Collared Lemmings in the Ogilvie Mountains represent a relic population of *Dicrostonyx* that became isolated on nunataks (unglaciated mountain tops) during the Last Glacial Maximum and that they may remain reproductively isolated. Although the Ogilvie Mountain Collared Lemming is afforded species status by Wilson and Reeder (2005), the taxonomic status of Collared Lemmings in the Ogilvie Mountains is unresolved (J. Eger, Royal Ontario Museum, personal communication).

The Ogilvie Mountain Collared Lemming is one of the least known terrestrial mammals in North America (Nagorsen 1998). Only 13 museum specimens exist, all collected from a single mountain, Trapper Mountain (64.583°, -138.217°), located in Tombstone Territorial Park, Yukon (Youngman 1964, 1967, 1975; Slough and Jung 2007). The specimens were collected at 1625–1676 m above sea level in dry rocky alpine tundra (heath) at the base of glacial cirques.

Limited survey effort has hampered our ability to assess accurately the distribution of this apparently range-restricted small mammal. Because surveys have been constrained by the remote high-elevation habitats in the Ogilvie Mountains, it is unknown whether this species is restricted to a single mountain. We conducted a targeted survey for the Ogilvie Mountain Collared Lemming to determine whether it inhabits other nearby mountains. This information is essential for better understanding the distribution and conservation status of this population.

Study Area

During 19–31 August 2011, we surveyed 12 mountains in the southern Ogilvie Mountains, all located within Tombstone Territorial Park. Tombstone Territorial Park is approximately 2,200 km^2, much of which lies above the tree line. Our sampling sites were distributed over five distinct mountain ranges (Table 1 and Figure 1). The mountains we surveyed were distributed throughout the park to provide spatial coverage of the alpine habitat within the park. We did not sample at Trapper Mountain because the species was already known from there (Youngman 1964, 1967, 1975; Slough and Jung 2007). Survey sites were accessed by helicopter.

Methods

On each mountain surveyed, we selected a sampling site in alpine tundra that was similar in elevation and habitat characteristics (dry heath, gentle slope) to capture sites on Trapper Mountain (Youngman 1975; Jung *et al.*, unpublished data). At each sampling site, we set snap-traps in variable-length trap lines that contained 60 trapping stations (49 in 1 case) set 10–15 m apart. At each trapping station, we set both a Museum Special and a Victor snap-trap (Woodstream Corp., Lititz, Pennsylvania) 1–2 m apart. Traps were baited with peanut butter and rolled oats and left unattended for 9–11 days ($\bar{x}$ = 10.3 ± 0.3 standard deviation [SD]; Table 1). We recorded the number of specimens captured per trap line and the number of traps that were

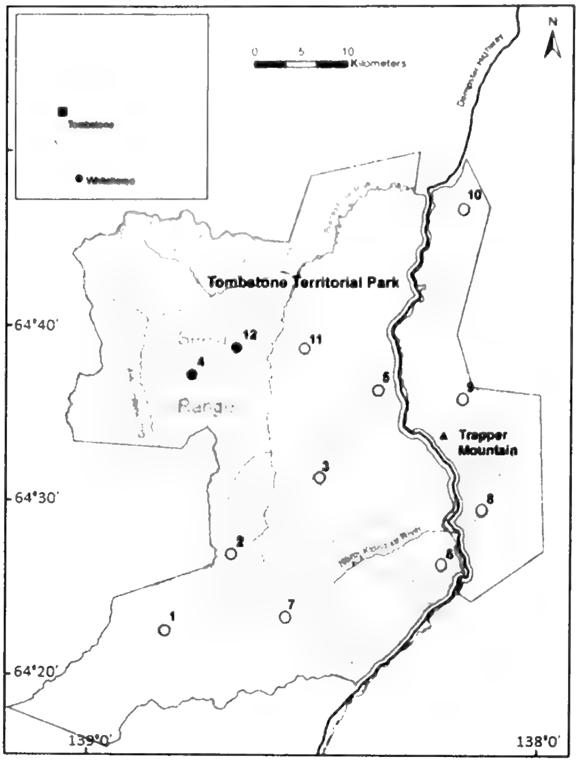

FIGURE 1. Boundaries of Tombstone Territorial Park, Yukon, Canada, and the 12 sites sampled for the Ogilvie Mountains Collared Lemming (*Dicrostonyx nunatakensis*) in 2011. Filled circles indicate locations where lemmings were captured, open circles where they were not detected. Note: Trapper Mountain is the only mountain where specimens were previously collected.

sprung or not functioning at the end of the sampling period. Our sampling protocol represented a maximum sampling effort of 14 638 trap nights (1 trap night = 1 trap set for 1 night).

Captured animals were identified by morphology and pelage. Small mammals were identified using the key provided by MacDonald (2003). Identification of the Ogilvie Mountains Collared Lemming was based on morphologic and pelagic characteristics, particularly very short tail and ears, densely furred feet, and buff-gray fur with a black dorsal stripe (MacDonald 2003). We deposited specimens at the Royal Ontario Museum (Toronto, Ontario).

Results and Discussion

Overall the number of animals captured was small: 26 captures of small mammals of four species, including three specimens of the Ogilvie Mountains Collared Lemming (Table 1). Ogilvie Mountains Collared Lemmings were collected from two of the 12 mountains surveyed, both in the Seela Range (Table 1). The two sites were 5.7 km apart and 25.9 km and 29.6 km west of previous collections on Trapper Mountain. Capture locations were among the most distant sampling sites from Trapper Mountain, and they were separated from

TABLE 1. Summary of site information, sampling effort, and trap captures during a targeted survey of the Ogilvie Mountains Collared Lemming (*Dicrostonyx nunatakensis*) in Tombstone Territorial Park, Yukon, Canada, August 2011.

	Site information				Sampling effort			Trap captures*			
Site	Mountain range	Latitude (°N)	Longitude (°W)	Elevation (m)	No. traps set	No. trapping nights	% sprung traps†	Ogilvie Mountains Collared Lemming	Northern Red-backed Vole	Tundra Vole	Montane Shrew
1	Tombstone	64.3923	138.8580	1551	120	11	76.7	0	4	0	1
2	Cloudy	64.4706	138.7239	1410	98	11	84.7	0	0	0	0
3	Cloudy	64.5510	138.5491	1558	120	11	86.7	0	0	3	0
4	Seela	64.6383	138.8532	1709	120	11	‡	1	3	0	0
5	Blackstone	64.6414	138.4342	1560	120	11	100.0	0	0	0	0
6	Tombstone	64.4789	138.2529	1696	120	12	60.8	0	1	0	0
7	Tombstone	64.4157	138.5951	1338	120	10	64.2	0	2	0	0
8	Prospector	64.5352	138.1742	1548	120	10	86.7	0	0	0	0
9	Prospector	64.6397	138.2427	1607	120	10	84.2	0	1	0	0
10	McFarland	64.8221	138.2845	1356	120	9	97.5	0	1	0	0
11	Blackstone	64.6703	138.6084	1630	120	9	75.0	0	1	1	0
12	Seela	64.6686	138.7590	1631	120	9	77.5	2	3	2	0

*Note: Northern Red-backed Vole, *Myodes rutilus*; Tundra Vole, *Microtus oeconomus*; Montane Shrew, *Sorex monticolus*.
†Traps set off without apparently capturing an animal.
‡No data.

Trapper Mountain by the Blackstone River, a potential barrier to dispersal (Figure 1).

Two Ogilvie Mountains Collared Lemmings were juvenile males and the other was a juvenile female. They were collected in dry heath type habitat at elevations (1631–1709 m above sea level; Figure 2) typical of previous captures at Trapper Mountain (Youngman 1967; Slough and Jung 2002). Vegetation at the capture sites was dominated by mountain avens (*Dryas* spp.), dwarf willow (*Salix* spp.), mosses, lichens (*Thamnolia vermicularis*, *Flavocetraria nivalis*), and grasses (e.g., *Anthoxanthum monticola*), along with other ericaceous species (e.g., *Arctous alpinus*, *Betula glandulosa*, *Empetrum nigrum*, *Cassiope tetragona*, *Vaccinium vitis-idaea*; Figure 2). Small mammal species caught in association with the Ogilvie Moun-

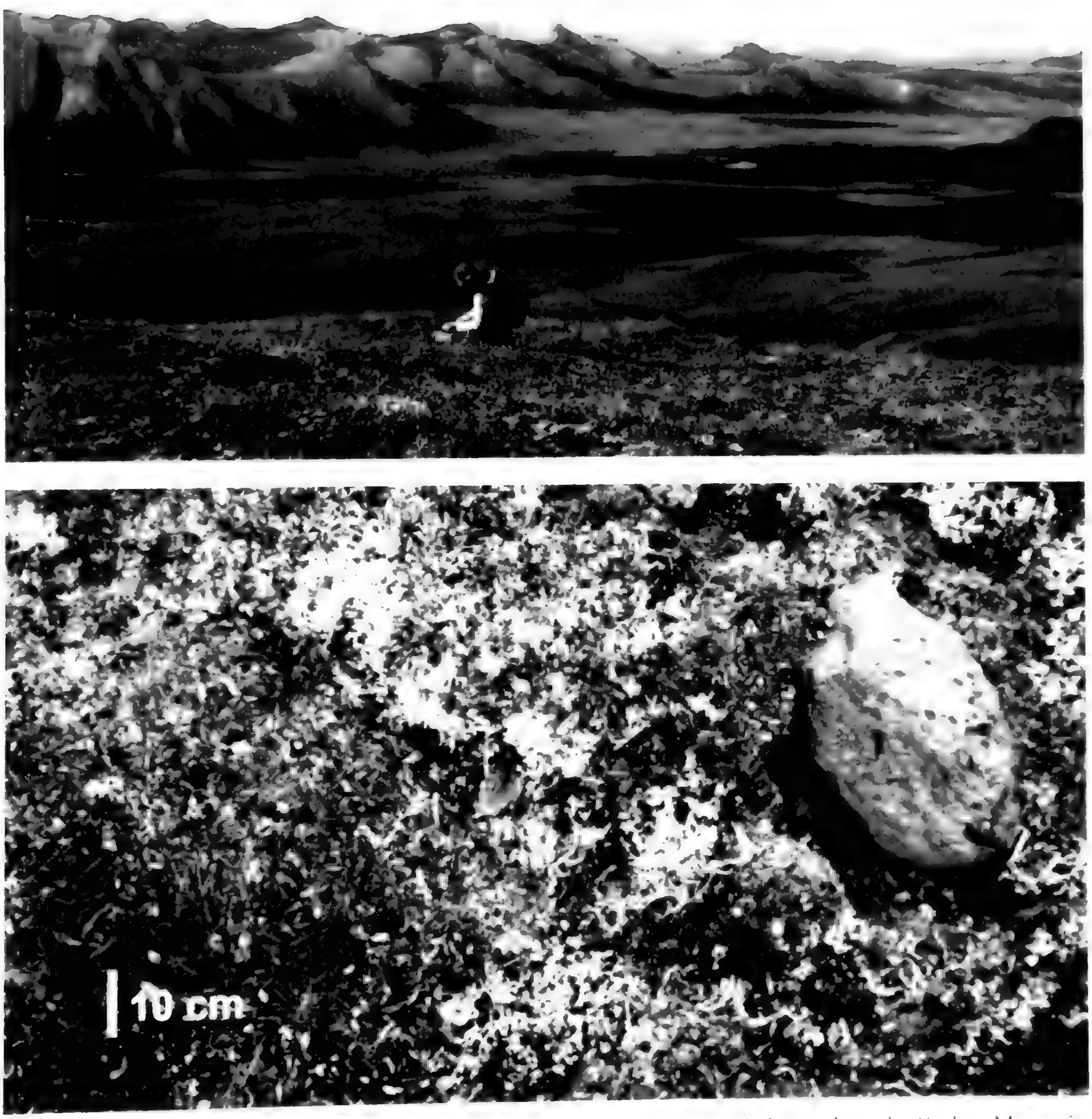

FIGURE 2. Landscape (top) and micro-site (bottom) views of the high alpine heath habitat where the Ogilvie Mountains Collared Lemming (*Dicrostonyx nunatakensis*) was collected in central Yukon, Canada, August 2011. Scale shown in the bottom panel is approximate. Photos: Brian Slough (top) and Thomas Jung (bottom).

tains Collared Lemming were the Northern Red-backed Vole (*Myodes rutilus*), the Tundra Vole (*Microtus oeconomus*), and the Montane Shrew (*Sorex monticolus*; Table 1).

Many traps ($\bar{x}$ = 81.2% ± 3.7% SD) were prematurely sprung or missing when we returned to check them (Table 1), which substantially reduced the sampling effort. Based on earlier survey work using the same trapping protocol in the study area (Jung *et al.*, unpublished data), we suspect that most traps were disabled early within the sampling period, resulting in the low number of small mammals captured. However, the time from deployment during which our traps were functional is unknown. Arctic Ground Squirrels (*Urocitellus parryii*) were abundant at all sampling sites, and we suspect that they were responsible for the vast majority of traps that were prematurely sprung or missing. For further surveys, means should be sought to reduce disturbance of traps by Arctic Ground Squirrels, such as placing a wire enclosure over the trap.

We confirm that Ogilvie Mountains Collared Lemmings are more widely distributed than solely on Trapper Mountain. We suspect that they were present on some of the 10 mountains we surveyed without detecting them. The habitat at all sites surveyed was similar. The functional loss of many traps likely resulted in a low sampling effort, hindering our ability to capture collared lemmings at some survey sites. The occurrence of Ogilvie Mountains Collared Lemmings on three mountains within the Ogilvie Mountains suggests that they may be somewhat widespread in suitable habitats there. Moreover, Youngman (1975) speculated that the Ogilvie Mountains Collared Lemming likely also occurs in the adjacent Wernecke and Selwyn Mountains of central Yukon, but there have been few (if any) small mammal surveys in these ranges. Further surveys are needed to delineate the range of the Collared Lemming within the Ogilvie Mountains and adjacent ranges.

Acknowledgements

We thank D. Amos, C. Eckert, and T. Powell for facilitating this work and assisting with field logistics. We thank L. Hughes, S. Hughes, M. Kienzler, and A. McCulley for field assistance. We thank J. Eger for discussions about collared lemmings and archiving our specimens at the Royal Ontario Museum. Two anonymous reviewers provided thoughtful comments on an earlier draft of this manuscript.

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Received 2 October 2013
Accepted 3 February 2014

A Note on Bird Song: Samuel Hearne's Observations on the Snow Bunting (*Plectrophenax nivalis*)

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Noakes, David L. G., and Jeffrey D. Noakes. 2014. A note on bird song: Samuel Hearne's observations on the Snow Bunting (*Plectrophenax nivalis*). Canadian Field-Naturalist 128(3): 269–271.

In 1795, the Arctic explorer Samuel Hearne recorded detailed observations on the distribution, ecology, molt, and behaviour of the Snow Bunting (*Plectrophenax nivalis*). The most significant of his observations was that Snow Buntings imitated the vocalizations of Atlantic Canaries (*Serinus canarius*) when housed with that species. His account has apparently not been widely recognized by ornithologists, but it is one of the first such observations on bird's acquisition of vocalizations.

Key Words: Arctic; bird song; Atlantic Canary; Snow Bunting; Samuel Hearne; *Serinus canarius*; *Plectrophenax nivalis*

Introduction

The study of avian vocalizations, especially their acquisition and development, is a central part of what is often recognized as "classical" ethology (Kroodsma and Miller 1996). Niko Tinbergen was one of the founders of ethology (Tinbergen 1951), and details of his field studies of Snow Buntings (*Plectrophenax nivalis*) in Greenland remain a classic (Tinbergen 1939; Dawkins *et al.* 1991). This note brings attention to an apparently unrecognized early description of the vocalizations of Snow Buntings in the written accounts of a European Arctic explorer, Samuel Hearne.

The species-typical nature of avian vocalizations has long been recognized and is the basis for field identification by expert field naturalists (Baptista 1975). Pernau is now recognized for attributing birds' acquisition of species-typical song to learning in the 16th century, but his observations are not widely known or generally appreciated (Birkhead 2003). Some of the earliest experimental observations on the acquisition of avian vocalizations were reported in the scientific literature by Barrington (1773). He hand reared young Linnet (*Carduelis cannabina*) and concluded that they acquired their vocalizations as a result of early exposure to those of adult birds. His experimental approach showed the way for many who followed (Kroodsma and Baylis 1982); however, it was not until recording and playback equipment became available that much progress could be made in the study of avian vocalizations (Baker 2001). The considerable advances in the study of avian vocalizations from the 1950s were a result of the use of equipment, especially the sonograph, that had been developed during World War II for detecting and recording sounds (Thorpe 1954).

Our understanding of the development of avian vocalizations is well past the classical studies of Marler (1952) and Thorpe (1954). Complexities of song acquisition include both auditory and visual cues, varying degrees of plasticity, dialects, vocal mimicry, and restricted learning (Brooke and Birkhead 1991). Detailed models have been proposed to account for song learning in birds, including instruction, selection, and instruction followed by selection in production (Marler 1997). However, what might appear to be simple descriptions of natural history observations, such as those by Hearne, are always valuable in any area of science. In this case, they document an important historical accomplishment that deserves credit in itself. They are also important as they may be useful to test the generality of our current hypothesis or suggest yet another interesting prediction to be tested in another species.

Historical Record

Samuel Hearne was one of the first European explorers in the region that is now part of the Canadian Arctic (Cavell and Noakes 2010). His writings (Hearne 1911) provide a wealth of details on numerous mundane aspects of daily routines as well as more unique events. He gave detailed accounts of the distribution and abundance of a number of bird species, mostly in relation to hunting them as food. However, he also remarked on the behaviour of Snow Buntings that he held as part of an extensive menagerie (Newman 1998). He described how they could be captured, or shot, at different times of the year, and he recorded that, when held in the company of exotic Atlantic Canaries (*Serinus canarius*), Snow Buntings learned to imitate the song of the canaries.

With reference to the vocalizations of Snow Buntings, Hearne wrote: "They live long in confinement, have a naturally pleasing note, and when in company with Canary birds soon imitate their song. I have kept many of them in cages in the same room with Canary birds, and always found they sung in Winter as well as in Summer; but even in confinement they change their plumage according to the season, the same as in a wild state" (Hearne 1911, page 386).

Unfortunately, his description lacks some valuable details. For example, the sex and age of the Snow Buntings, particularly as they might relate to song acquisi-

tion and development, are not given in his description. We now know from a wealth of detailed experimental studies a good deal about song development in Oscines, the group that includes the Snow Bunting (Marler 1997). We know that these birds develop their songs by learning early in ontogeny. It seems unlikely that Hearne would have reared Snow Buntings in captivity from the early age (about 20 days after hatching) that is required to demonstrate initial song learning. Thus, it would seem that he observed Snow Buntings changing their songs later in life, after they had acquired their species-typical songs in nature. There is evidence that some oscine species can change their songs later in life, as a result of exposure to vocalizations from other species (Marler 1990; Beecher and Brenowitz 2005; Laiolo *et al.* 2011).

Hearne's descriptions do not indicate whether his observations refer only to males or to both sexes of Snow Buntings. Females of some oscine birds do vocalize (Brenowitz and Arnold 1986). Hearne did not report whether the Snow Buntings replaced their song with the canary songs. He also does not provide any further details as to how he managed to hold the birds alive for such a long time under what were terribly demanding conditions for humans, let alone their domestic companion species (Newman 1998). Incredibly, he does not mention how or why he happened to have Atlantic Canaries available to him during his explorations of the North American Arctic!

Discussion

Hearne's Arctic accounts are widely and well known, but his observations of Snow Bunting vocalizations have not been noted before, despite reviews in the ornithological literature (Houston 1989). There is extensive literature on the domestication of the Atlantic Canary that dates from at least the 16th century. The songs of the canaries and their colours attracted a great deal of attention, and the birds were widely distributed by amateur bird keepers throughout Europe and Britain (Birkhead 2003). The 18th century European explorers who came to North America would certainly have been familiar with canaries, but it is remarkable that they brought them on their voyages (Houston *et al.* 2003).

Recent descriptions of the behaviour and ecology of Snow Buntings have included descriptions of their vocalizations (Thorpe and Lade 1961; Lyon and Montgomerie 1985, 2011;Espmark 1995, 1999; Alsop 2001; Hofstad *et al.* 2002; Meltofte 2007). Espmark (1995) concluded that the song of the Snow Bunting is stereotypic, as it is for most Emberizidae species. Alsop (2001) describes the song as "a series of bold repetitive high trilling notes," produced only on the breeding grounds. Snow Buntings are reported to have individual song patterns and Espmark (1995) concluded that there is no strong evidence of local song dialects. There has been no detailed study of the development of vocalizations in this species; thus, we do not know whether they learn their song by instruction or selection, nor do we know the period during which they can acquire their song. However, Hearne clearly deserves recognition for his insightful early observations on the development of behaviour, in addition to his broader contributions to our understanding of Arctic biology.

Acknowledgements

This note is dedicated to the memory of a friend and graduate classmate, Luis Baptista, who knew more about the languages of people and birds than anyone. We thank Dr. Doug Robinson, Oregon State University, and Dr. David Sherry, University of Western Ontario, for their reviews of an earlier draft of this manuscript. The detailed comments of anonymous reviewers and the editor significantly improved this manuscript and are very much appreciated.

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Received 31 October 2013
Accepted 10 February 2014

Late-winter Habitat Use by the Fisher, *Pekania pennanti* (Erxleben, 1777), in the Boreal Plains Ecozone of Northwestern Saskatchewan, Canada

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Proulx, Gilbert. 2014. Late-winter habitat use by the Fisher, *Pekania pennanti* (Erxleben, 1777), in the Boreal Plains Ecozone of northwestern Saskatchewan, Canada. Canadian Field-Naturalist 128(3): 272–275.

Late-winter habitat use by the Fisher, *Pekania pennanti* (Erxleben, 1777) in northwestern Saskatchewan was assessed in February 2009, 2011, and 2012. A total of 78 Fisher tracks were recorded over 60 300 m of snowshoe surveys. Fisher tracks were significantly less frequent than expected in Tamarack (*Larix laricina* [Du Roi] K. Koch) stands with > 40% crown closure and mainly 0–10 m trees ($P < 0.05$) and in open areas. Fishers used other habitat types equal to availability, including muskeg and coniferous, mixed, and deciduous forest stands. Maintaining mosaics of forest stands of different seral stages interspersed with muskeg would meet the late-winter habitat needs of Fishers in the Boreal Plains Ecozone of northwestern Saskatchewan.

Key Words: Fisher; *Martes pennanti*; *Pekania pennanti*; muskeg; Saskatchewan; winter habitat; Boreal Plains

Introduction

In western Canada, Fisher (*Pekania pennanti* [Erxleben, 1777]; formerly *Martes pennanti*, Sato *et al.* 2012) habitat studies have been conducted in coniferous, mixed, and deciduous forests (Badry *et al.* 1997; Weir and Harestad 1997; Proulx 2006). However, none has been carried out in the Boreal Plains Ecozone of northern Saskatchewan, where treed fens and bogs (referred to as muskeg) are abundant and the Fisher is a species of economic importance because of its value as a furbearer and its role in supporting the subsistence of Aboriginal groups (Koback 2014*). The purpose of this study was to assess late-winter habitat use by the Fisher in northwestern Saskatchewan.

The study was conducted in Mistik's Forest Management Agreement (FMA) area, north of Meadow Lake (54°07'N, 108°25'W), adjacent to the Alberta border. The area encompasses approximately 1.8 million ha of forest, water, and non-forested land. It is a mosaic of upland deciduous and coniferous boreal forest, muskeg, and water (McLaughlan *et al.* 2010) resulting from frequent fires of various sizes and intensities (Parisien *et al.* 2004). The area lies within the Boreal Plains Ecozone where White Spruce (*Picea glauca* [Moench] Voss), Black Spruce (*Picea mariana* [Miller] Britton, Sterns & Poggenburgh), Jack Pine (*Pinus banksiana* Lambert), and Tamarack (*Larix laricina* [Du Roi] K. Koch) are the dominant conifers (Environment Canada 2008). Deciduous stands of Trembling Aspen (*Populus tremuloides* Michaux), Balsam Poplar (*Populus balsamifera* Linnaeus), and Paper Birch (*Betula papyrifera* Marshall) occur throughout the study area (Rowe 1972).

Field inventories were carried out in February 2009, 2011, and 2012. The range of temperatures was similar among years (0 to −30°C), but, based on monthly average temperatures for the region, the 2012 winter (−10.8°C) was slightly warmer than 2009 (−16.3°C) and 2011 (−16.5°C) (Munroe 2012*; Government of Canada 2014*). During inventories, snow depths ranged from 30 to 65 cm in 2009 and 2011, and 30 to 45 cm in 2012. The survey method followed Proulx (2006, 2011). A random-stratified approach (Krebs 1978) was used to locate linear transects averaging ≥ 1 km long and ≥ 1 km apart that crossed all habitat types. Different transects were surveyed from year to year. Transects were plotted on 1:15 000 scale maps, and starting points were located using compass bearings and distance to distinct photographic features. Transects were followed on snowshoes, using a compass and a hip chain (a device used to record linear distances). Transect lengths varied according to accessibility, safety, and environmental conditions (e.g., open water, unexpected snowstorm, etc.). I recorded only well-defined tracks: those not melted or deformed, not filled with crusty snow, and judged to be less than 48 h old (a subjective assessment based on my experience). Because Fisher and American Marten (*Martes americana* [Turton, 1806]) footprints are similar (Halfpenny *et al.* 1995), when mustelid tracks were encountered, I investigated both sides of transects and within forest stands to find the best tracks available. The combination of footprint (size, presence/absence of toe prints) and trail (gait, distance between jumps, and dragging of the feet) characteristics were used to identify all tracks (Murie 1975; Rezendes 1992; Halfpenny *et al.* 1995). I recorded the location of tracks as both linear distance along the transect and universal transverse mercator.

Autocorrelation is often present in ecological data and cannot be completely avoided (Proulx and O'Doherty 2006). It may occur during analyses of track survey data because of uncertainty whether one or more animals has made the tracks being counted. It is difficult to confirm that a series of tracks along a transect belongs to a single animal (de Vos 1951) as home

ranges overlap (Badry *et al.* 1997; Weir 2003), and winter dispersal movements are known to occur (Arthur *et al.* 1993). Because of rugged environmental conditions, I did not follow tracks that crossed close together to learn whether the same animal made them. On the basis of track characteristics, Proulx (2006, 2011) deduced that two different animals could be as close as 100 m along the same transect. To minimize spatial autocorrelation, a minimum spacing of tracks and a minimum spacing of transects were used (Proulx and O'Doherty 2006). Only tracks ≥ 100 m apart within the same forest stand were recorded as two independent tracks. Tracks < 100 m apart but in two different stand types were also recorded as two independent tracks (Bowman and Robitaille 1997; Proulx 2006).

The Silvacom Group (Edmonton, Alberta) produced 1:15 000 scale vector maps for data analyses, using Saskatchewan Forest Inventory Vegetation datasets (Saskatchewan Environment 2004*). Nearly half the total length of transects surveyed in 2009, 2011, and 2012 was in treed bogs and fens. Independent of their age, these habitats varied considerably in structure according to many factors, such as landscape position, origin, slope gradient, water table location, drainage, etc. (Smith *et al.* 2007). Habitat classes were, therefore, based on the vegetation composition (≥ 60% Black Spruce stands, ≥ 60% Tamarack stands, pure and mixed Jack Pine stands with less than 60% Black Spruce or Tamarack, and deciduous or mixed-coniferous-deciduous stands); crown closure (percentage of ground area covered by the vertical projection of the crown to the ground, 0–20%, 21–40%, or > 40%); and tree height (0–10 m, 11–20 m, or > 20 m) in the forest stands (Saskatchewan Environment 2014*). Crown closure values for deciduous stands refers to summer datasets; I considered crown closure to be 0% in winter. Crown closure values for coniferous stands were representative of stand conditions throughout the year. Winter crown closure data for mixed wood stands was corrected according to the proportion of deciduous species.

The proportion of habitat types traversed by survey transects were used to determine the expected frequency of tracks per habitat type if tracks were distributed randomly with respect to habitat types (Proulx and O'Doherty 2006; Proulx 2011). Habitat use (i.e., observed versus expected frequency of track intercepts) was tested using χ^2 statistics with Yates correction (Siegel 1956; Zar 1999). When χ^2 analyses suggested an overall significant difference between observed and expected frequencies, further comparisons were conducted for each habitat class using the G test for correlated proportions (Sokal and Rohlf 1981). Probability values ≤ 0.05 were considered statistically significant.

Transects crossed major habitat types: Black Spruce-dominated stands, 23.2%; Tamarack-dominated stands, 22.6%; other coniferous stands, 6.6%; deciduous stands, 18.4%; mixed wood stands, 22.9%; and open areas, 6.1%. A total of 78 Fisher tracks were recorded over 60 300 m of transects. There was a significant difference between observed and expected frequencies of tracks per habitat class (χ^2 = 18.7, df 9, P < 0.05) (Figure 1). No Fisher tracks were encountered in open areas, i.e., cut blocks, burns, roads, and pipelines. Tracks were significantly less frequent than expected in Tamarack stands with > 40% crown closure (G = 3.9, P < 0.05), which consisted mainly of 0–10 m tall trees. Fishers used other muskeg and coniferous, mixed wood and deciduous forest stands as available.

Fishers avoided open areas and Tamarack stands with > 40% crown cover and small trees because these stands do not have a well-developed understory (McLaughlan *et al.* 2010; G.P., unpublished). They offer relatively little ground structural complexity for prey and provide Fishers with little protection against weather and predators (G. P., unpublished). This finding is in agreement with previous studies in various ecozones (Proulx 2006; Lancaster *et al.* 2008; Weir and Corbould 2010).

In the Boreal Plains Ecozone, late-winter Fisher habitat may correspond to any forested area that provides suitable prey, as suggested for other ecozones by Strickland *et al.* (1982) and Arthur *et al.* (1989). In Mistik's FMA area, large forested areas dominated by Trembling Aspen were being used by Fishers, as was

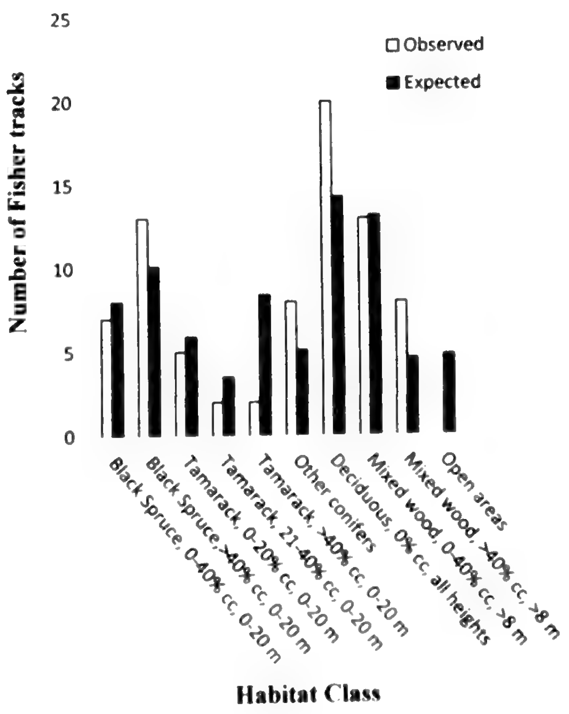

Figure 1. Observed and expected distribution of Fisher tracks (n = 78) by habitat class (including percentage crown closure [cc] and range of tree heights) in late-winter 2009, 2011, and 2012, Mistik's Forest Management Agreement area, Saskatchewan.

found in the Prairie Ecozone (Badry *et al.* 1997). In these ecozones, the presence of dense coniferous cover during winter may not be necessary when there is a well-developed understory. Fishers were found in deciduous stands and in muskeg where a lack of crown cover was compensated for by well-developed undergrowth (McLaughlan *et al.* 2010; G.P., unpublished), which may provide Fishers with homoeothermic advantages (Buskirk *et al.* 1989; Badry *et al.* 1997) and access to prey (Powell and Zielinski 1994). In treed bogs, Fishers investigated shrub thickets and the bases of trees, and their tracks were often associated with Snowshoe Hare (*Lepus americanus* Erxleben, 1777) trails (G.P., unpublished). Thus, this study suggests that conserving mosaics of muskeg interspersed with forest stands of diverse composition and structure would meet the late-winter habitat needs of Fishers.

Acknowledgements

This study was funded by Mistik Management Ltd. I thank Al Balisky, Kevin Gillis, and Roger Nesdoly of Mistik Management for their logistic support throughout the study and Neil MacKenzie and Kim Stang of Alpha Wildlife for field assistance. I am grateful to John Peters and Ryan Spooner from the Silvacom Group for the development of maps. I thank associate editor David Nagorsen and two anonymous reviewers for their comments on an earlier version of the manuscript.

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Received 12 February 2014
Accepted 9 April 2014

A Tribute to Warren Baxter Ballard, 1947–2012

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Cook, Francis R. 2014. A tribute to Warren Baxter Ballard, 1947–2012. Canadian Field-Naturalist 128(3): 276–288.

Warren Baxter Ballard, professor and Bricker Chair in Wildlife Management, Department of Natural Resources Management, Texas Tech University, Lubbock, Texas, lost a battle with pancreatic cancer on 12 January 2012.

He had gained broad research experience in wildlife biology in the boreal forest of Alaska in the northwest and New Brunswick in the east and very different habitats in the southwestern United States. In addition, he had been to New Zealand, Poland, Sweden, and Russia. His extensive publication record spanning 1971 to 2013 included 27 contributions to *The Canadian Field-Naturalist* covering a variety of vertebrate taxa, including ducks, turkeys, deer, caribou, foxes, wolves, and bears and usually coauthored with students and colleagues. His editorial contributions to journals and other publications were also extensive. As associate editor of *The Canadian Field-Naturalist* for mammals 1994–2001, 2007–2011, and before and between these periods as an occasional reviewer, he contributed over 280 individual reviews himself or assigned them to graduate students as part of their training.

Warren was born on 28 April 1947, in Boston, Massachusetts. His family moved to Albuquerque, New Mexico, in the early 1950s and Warren attended St. Pius X High School there and, subsequently, enrolled at New Mexico State University. He held numerous summer positions with the New Mexico Department of Game & Fish, the United States Army Corps of Engineers, the Bureau of Land Management, and the Department of Animal, Range and Wildlife Sciences, New Mexico State University. He obtained a bachelor of science degree in fish and wildlife management in 1969 and a master's in environmental biology from Kansas State University, Manhattan, Kansas, in 1971. His thesis for the latter was entitled, "Importance of social aggression in booming ground hierarchy of greater prairie chickens (*Tympanuchus cupido pinnatus*)"; his supervisor was Dr. Robert J. Robel.

From 1 August 1971 to 31 July 1973, Warren was a wildlife biologist with the U.S. Fish and Wildlife Service, Tulsa, Oklahoma. From 1 August 1973 to 1 November 1990, he was a research biologist with the Alaska Department of Fish and Game, in Juneau, Homer, Glennallen, Palmer, Anchorage, and Nome, Alaska, but resigned when his application for educational leave was rejected. From 11 January 1990 to 1 January 1992, he

Figure 1: Warren Baxter Ballard, about 2004, at Texas Tech University. Photographer Artie Limmer.

was a research associate at the School of Renewable Natural Resources, University of Arizona, Tucson He received a Ph.D. in Wildlife Science, University of Arizona, in 1993; his dissertation was "Demographics, movements, and predation rates of wolves in northwest Alaska" (supervisor: Dr. Paul R. Krausman).

Briefly, 1–10 January 1992, he was a wildlife research biologist with the U.S. National Park Service, Anchorage, Alaska. From 10 January 1992 to 1 July 1993, he was a senior wildlife ecologist with LGL Alaska Research Associates, Inc., Anchorage, Alaska. This was followed by a position as director and associate professor in the Cooperative Fish and Wildlife Research Unit, University of New Brunswick, Fredericton, New Brunswick, where he stayed until August 1996.

FIGURE 2. Warren Baxter Ballard and Heather Whitlaw on a visit to editor's residence in 2002. Photograph by Francis Cook.

Moving southwest, he spent 1 September 1996 to 1 February 1998 working as research supervisor, Arizona Game and Fish Department, Phoenix, Arizona. In a final move, from 7 January 1998 to 31 August 2003, he was an associate professor in the Department of Natural Resources Management at Texas Tech University, where he became associate chair on 2 July 2002 and was elevated to professor on 1 September 2003. On 13 April 2006, he was appointed to the prestigious Bricker Chair in Wildlife Management, a position he held until his death. In addition, he held appointments as adjunct professor, Faculty of Biology, University of New Brunswick (9 January 1993) adjunct associate professor, School of Renewable Natural Resources, University of Arizona, Tucson (1 October 1996), an adjunct to faculty, Division of Biology, Kansas State University, Manhattan (1 September 1998).

A highly regarded teacher, Warren taught seven courses over 39 terms achieving a 4.5 out of 5 rating in student response. He supervised 44 graduate students (30 at the M.Sc. level and 14 Ph.D.s) as well as two postdoctoral students.

A prolific writer and supervisor, Warren wrote or co-wrote an ever-increasing multitude of journal papers, monographs, contributions to books and conference proceedings, and miscellaneous publications, as well as invited presentations and progress reports which were not published.

His editorial contributions were numerous: in addition to his long service as associate editor of *The Canadian Field-Naturalist* mentioned above, he served as editor in-chief of *The Wildlife Society Bulletin* (2002–2005). He was co-editor of *Alces* (1998–2001); *The Moose Call*, the newsletter of the North American Moose Conference and Workshop, Canada (1994–1996); and the Third International Moose Symposium, Soviet Union (1991–1992). He was consulting editor for the University of Alberta Press (1992) and associate editor for *Wildlife Monographs* (2007, 2004, 1995–1996, and 1989), *The Wildlife Society Bulletin* (1998–2001), and *Alces* (1996–1997). He carried out peer reviews for the *Canadian Journal of Zoology*, the *Journal of Mammalogy*, the *Journal of Wildlife Diseases*, *The Journal of Wildlife Management*, *Alces*, the *Proceedings of Desert Bighorn Sheep Council*, the *Proceedings of the Second International Wolf Symposium*, International Bear Conference, *Ecoscience*, the *Journal of Range Management*, Texas Tech University Press, *Biological Conservation*, *Science of the Total Environment*, the *Texas Journal of Science*, and the *European Journal of Wildlife Research*.

Diverse awards have recognized Warren's many contributions: Distinguished Moose Biologist Award from the North American Moose Conference at St. John's, Newfoundland (1989); an Award for Excellence from the School of Renewable Natural Resources, Uni-

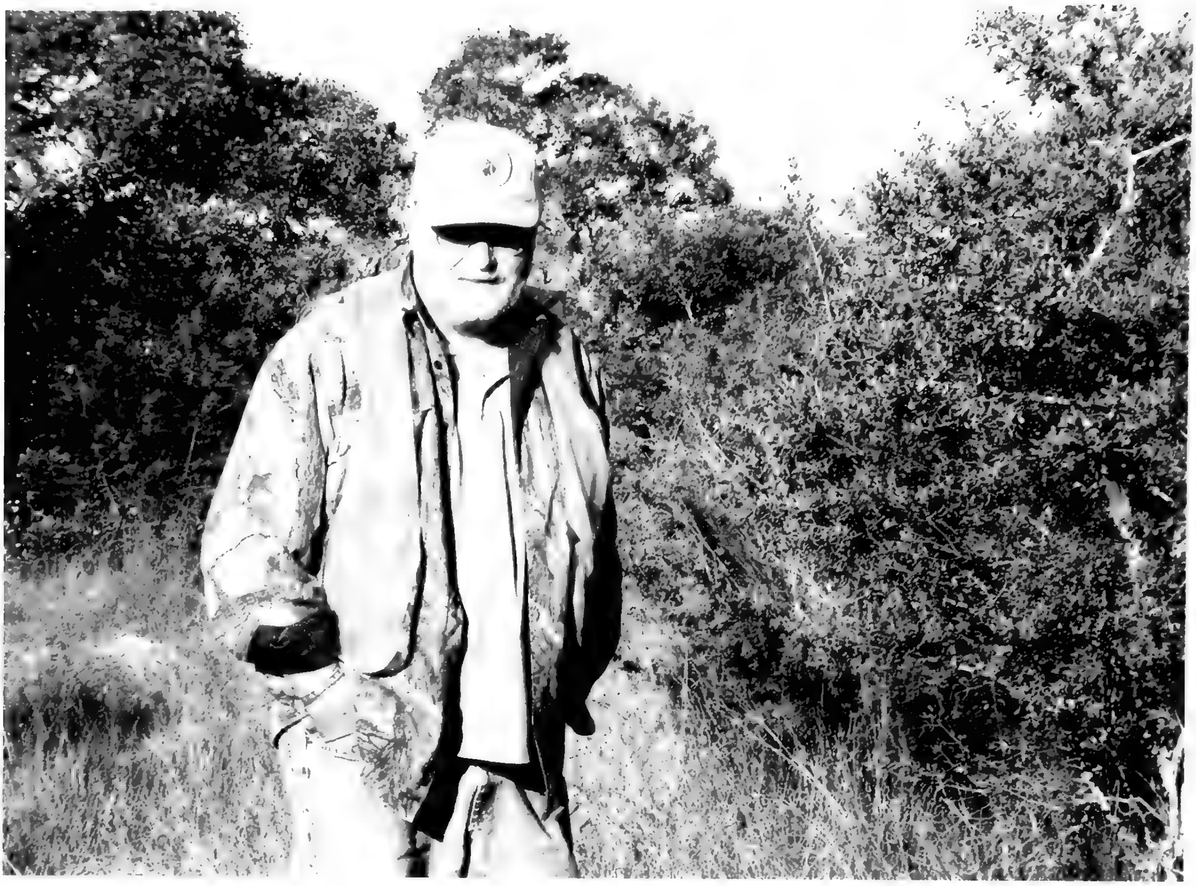

FIGURE 3. Warren Baxter Ballard on a hunting trip in Texas, October 2003. Photograph courtesy Heather Whitelaw.

versity of Arizona, for an outstanding dissertation (1994); the Order of Alces at the 31st North American Moose Conference for service to *Alces* (1995); a Special Service Award from the University of New Brunswick for contributions to the New Brunswick Cooperative Fish and Wildlife Research Unit from 1993 to 1996 (1996); admission to Sigma Xi honorary research fraternity (1999); the Big 12 Faculty Fellowship from Kansas State University (1999); a Teacher of the Year award from the Range, Wildlife, and Fisheries Club, Texas Tech University (1999); an Outstanding Researcher Award from the College of Agricultural Sciences and Natural Resources, Texas Tech University (2002); Best Article for 2002 from The Wildlife Society in Bismarck, North Dakota, for his paper entitled "Deer–predator relationships: a review of recent North American studies with emphasis on mule and black-tailed deer" (2002); a Special Service Recognition Award from The Wildlife Society, Bismarck, North Dakota (2002); a Chancellors Council Distinguished Research Award from Texas Tech University (2002); the life-time title of TWS Fellow from The Wildlife Society, Madison, Wisconsin (2005); an Outstanding Achievement Award from the Texas Chapter of the Wildlife Society, Beaumont, Texas (2006); and a Best Monograph award from The Wildlife Society for a manuscript entitled "Pathogens, nutritional deficiency, and climate influences on a declining moose population" authored by Dennis L. Murray, Eric W. Cox, Warren B. Ballard, Heather A. Whitlaw, Mark S. Lenarz, Thomas W. Custer, Terri Barnett, and Todd K. Fuller, Tucson, Arizona (2007).

Warren was exceptionally active in the science community and professional societies. He held professional membership in The Wildlife Society, the Texas chapter of The Wildlife Society, the American Society of Mammalogists, the Canadian Field-Naturalist, Sigma Xi, and the Southwestern Association of Naturalists. He held numerous positions on committees and served as a consultant to the University of Minnesota, the British Columbia provincial government, LGL Alaska Research Associates, Inc., Entrix Inc., and Revett Silver Mine concerning grizzly bear issues.

Warren had definite views on wildlife research and education, which he put into practice in his teaching, editing, and society involvement, as well as his own research. In his curriculum vitae, he stated,

> The purpose of wildlife research is to test hypotheses, develop better techniques, and build a sound database for the management and conservation of wildlife throughout the world. Wildlife research should always use and follow the scientific method. Research should be oriented both towards testing theory and solving technical problems. Dissemination of research results through

> publication is essential to a successful and productive research program.

> Education in wildlife and biological sciences should provide students with basic concepts and theories, and equip them with the necessary tools of the trade to be productive biologists. Knowledge of ecological concepts, effective communication skills, statistical expertise, and critical thinking should be stressed at all levels of college education. In addition, recent and current research, as well as management findings and problems should be incorporated into the education process.

On Warren's death, Texas Tech president, Guy Bailey, wrote, "Dr. Ballard was a Texas Tech Horn Professor and the Bricker Chair in Wildlife Management. A Horn professorship is the highest honor a faculty member can receive from the university. Horn professors are a testament to the quality of our academics because they represent the very best of our faculty."

"His legacy lives on in the students, faculty and research projects he touched," said Michael Galyean, interim dean of the College of Agricultural Sciences and Natural Resources.

"Warren was my friend since graduate school, an internationally-recognized research scientist, a major figure in this wildlife program, and an irreplaceable part of our department," said Mark Wallace, chairman of Tech's Department of Natural Resources Management.

On 18 January 2012, Canadian colleague, Graham Forbes, posted a note on a "tribute wall" (Lake Ridge Chapel and Memorial Designers postings): "Warren was very well-liked here at the University of New Brunswick during his time as director of the Wildlife Coop Unit. He initiated some great projects and was valued by all who worked with him. We missed him when he left UNB and it's hard to acknowledge he has passed. I presently occupy his old office and just had a large shot of whisky, in his memory, and his honour. Our thoughts are with Heather."

Dwayne Sabine also posted a message in January: "I was Warren's first grad student. I led one of two deer studies he initiated here in New Brunswick, Canada, and he hired Heather to run the other…. Warren was certainly a positive influence on my career and life. I have fond memories of time spent in the field and at camp with Warren and Heather. He always had great stories at hand, and (unfortunately, perhaps) I may have given him one or two more during his time here (the blindfolded deer that 'got away' comes to mind...)."

Graham Forbes recalled an additional anecdote from Warren's time at the University of New Brunswick (personal communication 18 February 2013): "Warren became 'known' to campus security one autumn when he took his Wildlife Investigation Techniques class on to the rugby field on the edge of campus for some drug immobilization training. The class was target practising with some Cap-Chur rifles (CO_2-powered for tranquilizing projectiles); in hindsight, it would have been prudent to inform security first!"

Personally, I will miss our many exchanges on manuscript evaluation and on life over 30 years. Our last conversation was shortly before he died — a comparison of our success with walkers. Warren, who had worked efficiently and productively with little interruption over several health setbacks, was ever upbeat and proud of his dexterity with his walker and encouraged me to improve with mine.

Warren was predeceased by his father, Warren Baxter Ballard. He was survived by his mother LaVerne Rosemary Ballard (née Bernat) and his wife, Heather Whitlaw, as well as children Cynthia Bergamo (husband Greg Bergamo), Warren B. Ballard, III (mother Ms. Sheila Sturtz), Laurina Wittig (husband Thomas Wittig), and Raymond Ballard (mother Ms. Tina Cunning); grandchildren Ezra Bergamo, and Blair and Brandon Ballard; mother-in-law, Nan McGhee, father-in-law, David Whitlaw, sister-in-law, Patricia Whitlaw; and nieces, Elizabeth and Paige Jones. He is fondly remembered by graduate students from the several universities where he had been a staff member as well as by research colleagues and friends from around the world.

Acknowledgements

Warren's wife and frequent coauthor, Heather Whitlaw, provided Warren's 2007 comprehensive curriculum vitæ, an updated 2012 list of Warren's publications, and a photograph. Roger Applegate searched for the full citation for many incomplete references to publications that appeared after Warren's death. At Texas Tech University, Kristina Woods Butler, Research and Academic Communications, Office of the Vice President for Research, and Norman Martin, College of Agricultural Sciences and Natural Resources, traced the source of Figure 1 and approved its credit and use, respectively. The notice in *The Lubbock Avalanche-Journal*, 13 January 2012, and online comments posted on the Internet guest book of Lake Ridge Chapel and Memorial Designers, 6025 82nd Street, Lubbock, Texas were drawn upon for additional information. Also accessed was the article by Roger D. Applegate and Paul R. Krausman. 2012. Warren B. Ballard, Jr. 1947–2012: A personal tribute. *The Wildlife Society* 36(1): 4–5. Roger Applegate, Graham J. Forbes, and Heather Whitlaw read earlier drafts of this article and made many appreciated corrections and additions.

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Received 5 February 2013
Accepted 10 March 2014

A Naturalist for All Seasons: Richard Merrill Saunders, 1904–1998

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Collins, Philip. 2014. A naturalist for all seasons: Richard Merrill Saunders, 1904–1998. Canadian Field-Naturalist 128(3): 289–294.

The year 2014 marks the 110th anniversary of Richard Saunders' birth and this tribute invites the reader to discover, or rediscover, something about the life of this popular ornithologist.

> The lure of the unexplored, the beckoning finger of novelty — what field naturalist can pass them by? The chance of finding a new bird, a new flower, the hope of having a new experience with some old friend of the wild in a new setting — these are sure enticements to send the ardent naturalist afield in search of adventure.

Saunders wrote these words in 1945, and they indeed sum up this ardent naturalist, who spent most of his long life observing the birds and wildflowers of Canada and beyond. The natural world, however, was not the vocation for which he had trained. As a professor of history, he taught at a number of universities for over 40 years, during which time he published several academic papers. Had this been his only achievement, he could still be considered to have made a worthy contribution to society. But there was another side to the man: his love of nature and his joy in communicating and sharing it with many people. It is for this that he most deservedly should be remembered.

Richard Merrill Saunders was born on 16 November 1904 in the bustling fishing port of Gloucester, Massachusetts, where his father, Lee Saunders, was in the catering business. Two years later his parents' marital problems reached crisis point and his father left the family home. His widowed maternal grandmother lived in Worcester, 60 miles to the east and it was there that his mother, Grace Merrill Saunders, together with Richard and his younger brother, Carroll, moved after the breakdown of the marriage. To provide for her family, Grace lived in Boston, where she worked full-time as a secretary in what was then predominately a male-dominated world of business, while her son was looked after by his grandmother, Sarah Jane, and a bachelor uncle who was the boy's masculine influence. To break the family up still further, his brother was looked after by a family in Quincy. It says much for Saunders' character as a youth and a teenager that, under those unusual family arrangements, he successfully completed his schooling in Worcester and, having decided on a teaching career, he entered Clark University as an undergraduate in 1920, obtaining his bachelor's degree four years later at the age of 20 and his master's the following year.

FIGURE 1. Richard Saunders c 1935.

He began his long academic career, not in the United States, but in distant Beirut, Lebanon, at the American University, where he taught history. It was an appointment that was to change his life in a most unexpected way. Unbeknown to him, Dr. West, one of the professors at the University had died leaving a family of six children in the care of his widow. She had remained at the campus and had eventually become the housekeeper for the entire University. She must have been a resourceful woman for she put all six children through Ivy League universities or Seven Sisters institutions.

One of her daughters, Anne, had just completed her studies at Vasser College in New York when Saunders met her on board ship as she returned to Beirut. It proved to be the happiest of meetings, and it soon blossomed into courtship. While in Beirut (despite a bad

bout of malaria), Saunders made a number of visits to Europe, including France, where he purchased a beautiful Sèvres vase for Anne, a gift which must surely have made a large hole in his pay packet but which must equally have impressed her hugely. They married in June 1929 at South Kent, Connecticut, having left Beirut and settled back in the United States in Ithaca.

Shortly afterwards, Saunders took up a post teaching history as a Boldt Fellow at Cornell University in New York. During this time, he studied for and in 1931 achieved his Ph.D. What followed next is recalled by his daughter:

> It might be wondered how an American ended up at a Canadian university. When father completed his Ph.D. it was deep in the Depression. He sent resumes to all the universities in North America and got no replies. One day Mother was house cleaning and picked up the rug in front of the door that had the mail slot. Under the rug was a letter from the University of Toronto saying they would accept Father, but they needed to know the next day! Needless to say, an expensive phone call was made immediately.

The couple moved to Toronto in 1931, where Saunders accepted the position of associate professor of history at the University of Toronto, specializing in the Age of Enlightenment European history. There he remained until his retirement from academia in 1970.

Such are the bare facts of the career of this energetic and much-loved teacher. But what of the man himself, and what sparked off a parallel career in natural history? He provides a slight clue in a book recounting his visit to South Carolina. Describing the experience of being mobbed by Least Terns (*Sterna antillarum*), he likens it to a similar encounter with Common Terns (*S. hirundo*) in Massachusetts. From this, we might deduce that his interest dated from his childhood or teens there. By 1938, however, he had become sufficiently well known and respected in Toronto ornithological circles to be invited to become the editor of the Toronto Field Naturalists' newsletter, a position he held for 27 years.

During the war, he continued to teach at the University, publishing several academic papers on aspects of French Canada, (although he always considered himself a teacher first and a writer second) and of course continuing his birdwatching. This latter activity was not without its risks; having a pair of binoculars around your neck and being in the vicinity of what are now termed "sensitive installations" was a recipe for trouble. On more than one occasion he was apprehended and interrogated in the local police station. Experiences like this were common among the birding fraternity in the early war years, such was the fear of spies. However, as time went on the birdwatchers became known to the police, who treated them at best with interest and at worst as harmless eccentrics.

Flashing Wings appeared in 1947, the year Saunders became a committee member of the American Ornithologists' Union, speaking at a dinner they held in Toronto. Far from being the only book he published (there were at least a dozen more titles covering historical and natural history subjects), it is perhaps the most unintentionally autobiographical. Tucked away in its pages are various clues and insights into some of his other talents. For example, speaking of the value of learning bird calls, he says: "Probably my own musical training gave me an advantage." He was a good pianist, but he suddenly gave it up in the late 1940s because the pressure of his work (and no doubt his constant birdwatching) did not allow him to keep practising to his satisfaction. However, he was interested in encouraging his students to know and appreciate music from the period he taught, and they would gather in his house to listen to records of Mozart and Haydn.

FIGURE 2. Saunders with Sally, his daughter, strawberry picking at Orangeville in 1944/5.

His book covers the period from 1934 to 1946, 12 years that saw him combining a busy program of teaching at the University with his passion for the outdoors and the birds of his adopted city of Toronto. One of the great virtues of Saunders' writing is his power to evoke landscape. There is a passage at the beginning of the book in which he details a snow-covered wood of hemlock trees near Maple where he watched Red Crossbills (*Loxia curvirostra*) and White-winged Crossbills (*L. leucoptera*) moving from branch to branch feeding. It is a magical description. He was a man clearly sensitive

to the beauty of nature and more than once observed that no artist could possibly do justice to the scene in which he was birding. For three of those 12 years he was president of the Toronto Field Naturalists, a further indication of the esteem in which he was held. During this time he also experienced first extreme happiness with the birth of Sally his daughter and then extreme despair when his four-year-old son Alan died from leukemia. This affected Saunders in an unimaginable way, creating within him a sort of denial (henceforth, he rarely mentioned his son's death) driving him to find solace in his field trips with the Toronto Field Naturalists and his work at the University.

He recounts in *Flashing Wings* many of those field trips he led, prompting George Bryant to recall recently:

> On Wednesday mornings, when I was a child my friend and I would cycle to Cedarvale Ravine before school where Saunders led weekly early morning spring migrant walks. He was a professor of history and had a most commanding presence. His voice was resonant, mellifluous and instantly recognisable.

Another participant on these May morning walks was Bruce Falls who recalls: "[Saunders'] deep resonant voice could be heard calling out the names of the birds he heard and observed for the benefit of his flock of devoted followers," later adding, "he was an enthusiastic, indeed exuberant birdwatcher," and, "one of the most active and best known birders of his day."

His appearance at the field trip meetings was imposing — leather jacket, breeches, high laced-up boots, and fur hat in the winter or, on other occasions, French beret, shirt with special plaid tie, and wool jacket. He was a naturalist for all seasons and an ornithologist for all weathers. In November, he writes with gentle censure, "The woods are empty of watchers. They are at home, no doubt, sleeping away the winter like the bear — hibernating naturalists!"

His daughter, who frequently accompanied her father on his birding trips, comments that her father spoke as he wrote, whether it was trying to get people to see a bird or to conduct a lecture, or both, as on one occasion while he was taking a tutorial he suddenly asked his students to put on their coats and go out into Queen's Park to see a Great Grey Owl. Falls, who was professor of zoology at Toronto recalls:

> I was surprised to learn that some of his colleagues in the Department of History regarded Professor Saunders as rather retiring. Apparently they had not attended his lectures that were animated and forceful. He sometimes appeared in period costume to heighten the drama.

Being in his presence must certainly have been an exciting experience. Sally recalls that during a lecture on Martin Luther, her father became so enthusiastic when recounting how Luther had nailed his "Ninety-five theses" to the door of the chapel in Wittenberg, Germany, that he stamped his foot so hard it went clean through the floor boards of the lecture room. Other

FIGURE 3. Saunders with his wife Anne in 1947.

examples of his humour surface from time to time in his writing, such as when he mentions his birdwatching — although unrelated namesake — W. E. Saunders:

> How old Mr. Saunders gets around. He is seventy-four and he goes everywhere and all the time to see his birds — down to Kingsville, up to Toronto and over to Hamilton all in one week. Quite a record for an old man. But he is not an old man! His birds and flowers keep him young; a retired business man but what a one. Most of them die of boredom and golf. He lives.

Flashing Wings chronicles a quite astonishing coverage of bird life in and around Toronto. In those days, the city was much smaller than it is now although there were signs of what was to come with his frequent references to building concessions and the loss of habitat. However, *all* has not been lost, and some of the areas that survive include Saunders' beloved Cedarvale Ravine (although parts have been lost to a subway station), Scarborough Bluffs, and Grenadier Pond. To read this book is to walk through a vanished landscape, but one that is described so accurately that one might be watching a documentary film about it. The book includes 37 fine drawings by his friend Terence Shortt (1911–1986). Shortt was then artist-ornithologist with the Division of Birds at the Royal Ontario Museum, becoming, in the year after *Flashing Wings* was published, chief artist of the Department of Art and Exhibits. In an appendix, Saunders also includes what is almost cer-

tainly the first table of arrival and departure dates of birds in the Toronto region, which is based on his and Jim Baillie's observations, making it a significant contribution to the ornithology of Ontario.

Saunders seems to have integrated his academic and the ornithological activities well, particularly after purchasing a house on McMaster Avenue, in a leafy Toronto suburb; it became the family home until he left it the year before his death. Many are the observations he made of birds seen during the mile or so walk to and from the university, and it was there that he wrote his next book *Carolina Quest*, published in 1951. It describes a birdwatching trip to South Carolina with Thomas Murray, a student in modern history at the University of Toronto and an active birdwatcher in the young group that birded with the Toronto Field Naturalists.

Although it was written four years after *Flashing Wings*, *Carolina Quest* in fact chronicles a visit to South Carolina made in June 1936 when Saunders was 32 years old. The earlier book had been well received, a fact which no doubt prompted him to build on its success. The narrative in the first section of *Carolina Quest* is a fine evocation of life and landscape in the Deep South, culminating in a brief but unforgettable sighting of a pair of Ivory-billed Woodpeckers (*Campephilus principalis*), thus numbering him among the small band of ornithologists who have seen this birdwatchers' Holy Grail, a bird now almost certainly extinct. The 12 beautiful woodcuts in the book are by Sylvia Hahn (1911–2001) who was the daughter of the artist and teacher, Gustav Hahn, and the sister of Saunders' secretary at the University. In 1934, she had joined the staff of the Royal Ontario Museum, to which she dedicated almost her entire artistic and amazingly versatile career. The final chapters deal with some of the birds that, in the past, had seemed so characteristic of the South and which were now increasingly to be found within the borders of Canada, thus providing an avian bond between the "Dominion of the North" and the "Deep South." A hint of things to come occurs when Saunders cites global warming as a possible factor for this expansion. He also includes what must be one of the earliest (and most humorous) descriptions of a full-blown "twitch" (numbering 80 birders) when a King Rail (*Rallus elegans*) appeared at Catfish Pond, High Park in Toronto.

The 1960s saw a quite radical decision made in the Saunders household. Having lived in Canada since they were married, Richard and Anne had grown used to, and now preferred, the Canadian way of life and so chose to take the nationality of their adopted country — although in those days it was a requirement that in so doing they had to relinquish their American citizenship. They felt that having Canadian passports made travel easier, particularly as America was then heavily involved in the Vietnam War, a fact that may well have contributed to their decision.

They were soon to make good use of these new passports, as Saunders, accompanied by Anne, took a sabbatical from the University, first visiting Europe, then the United Kingdom, travelling by steamship. For several weeks, they journeyed around Europe, mainly in France, a country whose language he spoke fluently, before crossing the channel to England. Here they stayed for four months while Saunders undertook historical research. Nevertheless, he still found time to make many field trips and to meet and become acquainted with Britain's ornithologists and discover its birds. The second part of the sabbatical was spent back in North America, driving down the east coast to Florida then continuing west to California, before turning north to Vancouver, taking in Yellowstone Park and the Canadian Rockies and returning home to Toronto. As her husband had never learned to drive, this challenging itinerary was undertaken by Anne.

Resuming his University duties, Saunders recalled how on one occasion his authority was challenged:

> In a fourth-year seminar in Sidney Smith Hall a girl arrived one afternoon, sat down and took out a nice black pipe which she proceeded to light up and to puff boldly, cocking an eye at me every so often. The rest of the group also watched to see what would happen. As it was obvious that, in the spirit of that day, she was trying to push me into some sharp reaction I decided to pay no attention at all and carried on the group discussion as usual. As it worked out she never tried anything like it again and proved to be a very good and attentive student. Nonetheless, she defied the professor and had done her own thing in good 1960s style.

Saunders' calm and experienced approach to handling this situation says much about his character.

In 1965, he relinquished his position as editor of the Toronto Field Naturalists' newsletter, bowing out with a résumé of the activities of that lively institution, which he published in the 26-page booklet *Toronto Field Naturalists' Club — Its History and Constitution*. He retired from academic life a few years later, having become increasingly afflicted by deafness which also dramatically reduced his birding activity. Bird identification through birdsong had always been his strength, and he once observed that when springtime arrived with its heavy foliage, 75% of bird observing was done by the ears.

To compensate for the onset of deafness, there were the wildflowers — an area of natural history that had interested him as a photographer since his meeting with Mary Ferguson in the late 1960s at the Toronto Photographic Club. She had a deep knowledge of flowers, and they had an immediate rapport. Mary's husband was a professor in the Department of Pharmacy at the University and the Saunders and Ferguson families soon became close friends. They began to go on field trips together and were frequent guests at the Fergusons' cottage on the shores of Lake Huron at Georgian Bay.

In 1973, the two families' most extensive journey together took them, this time by aeroplane, on an extended tour of Europe across France, Germany, Austria, and Switzerland. It is regrettable that Saunders never turned this trip (or indeed that made on his sabbatical) into a book. While in Europe, it is likely that plans were discussed with Mary, which resulted in the joint production of two books, *Canadian Wildflowers* (1971) and *Canadian Wildflowers through the Seasons* (1982). In the preface to the latter, Saunders wrote:

> The discovery of a rare or unusual flower, a new species… or an expanse of flowers in fields, woods or swamps exhilarates and spurs us on. We forget the swarming black flies and mosquitoes, the difficult progress into a bog or the tiring climb up a mountain trail…. When you go out with the same purpose, take along patience and perseverance as part of your equipment, and take pictures for the joy of it.

Note how his words, "the discovery of a rare plant or unusual flower," echo those quoted in the opening paragraph of this tribute: "the chance finding of a new bird." Saunders was very much an active, rather than a passive naturalist.

His contribution to ornithology and conservation can be summed up in those four last words from the preface quoted above: "for the joy of it." He communicated that joy in an infectious yet authoritative way, and in so doing introduced a great many people, both young and old, to a lasting enjoyment in studying birds.

The final decade of Richard Saunders' life was totally overshadowed by his wife's suffering a severe stroke which confined her to hospital until her death in 1993. They had been happily married for 64 years. Now profoundly deaf, and at his request, Saunders spent his last year in a senior retirement home close to his daughter where, sitting on his veranda, yet unable to hear his beloved birds, he could at least enjoy the sight of them at the feeders. After a short illness, he died in a hospital in Huntsville on 25 July 1998 aged 93 and is buried in the family grave in his beloved adopted city of Toronto.

That he was an *interesting* man is without question, and interesting people must never be allowed to sink into oblivion. If this tribute has opened a small window onto his life and stimulated others to research it still further, then it will have achieved its purpose. Let the final words be from the man himself:

> Often people ask me why I continue to look at the same birds week in and week out, year after year. Somehow they don't seem to realise that a sort of friendship springs up between observer and birds. And whoever comes to the end of wanting to see friends and to learn more about them?

Acknowledgements

The author gratefully acknowledges the invaluable advice, support, and recollections of Richard Saunders' daughter, Sally Saunders, who also made available the photographs. Thanks are due also to Margaret McRae, president of the Toronto Field Naturalists (TFN) for her helpful information and for enabling the initial contact to be made with Sally; Marilynn Murphy, formerly on the TFN newsletter committee; George Bryant and Bruce Falls for their recollections; and Sandi Kane of Clarke University Massachusetts and Michel Duquet of the Canadian Historical Association.

Figure 4. Anne Saunders favourite photo of her husband. Late 1960s.

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Received 2 April 2014
Accepted 25 April 2014

Associate Editor's Footnote

R. Saunders should not be confused with two unrelated W. Saunders, who are familiar to many Canadian naturalists.

"Known as Will or W.E. (short for William Edwin), W. E. Saunders was born in 1861, second in William Saunders' family of one daughter and five accomplished sons. The senior Saunders later became founding director of the Dominion Experimental Farm in Ottawa.

"Of the brothers, only W.E. remained in London, where he operated a wholesale pharmaceutical company until his death in 1943. Saunders' broad-ranging interests found outlets in civic, historical, horticultural, educational and musical circles." From Wake, Winnifred. 2011. W. E. Saunders, London's beloved naturalist. *Londoner* 18 October. Available: www.thelondoner.ca/2011/10/18/w-e-saunders-londons-beloved-naturalist (accessed 19 May 2014).

Will Saunders was a major part of the early naturalists group active at Point Pelee as partly documented by a later University of Toronto historian who included many references in *A Life with Birds: Percy A. Taverner, Canadian Ornithologist, 1875–1947* by John L. Cranmer-Byng. Canadian Field-Naturalist 110(1): 1–254 (1996).

For information about W. Saunders, senior, see Cody, W. J., D. B. O. Saville, and M. J. Sarazin. 1986. Systematics in Agriculture Canada at Ottawa 1886–1986. Agriculture Canada Historical Series number 28. 81 pages.

About the Author

Philip Collins lives in the United Kingdom and has been bird watching since childhood. He was a member of the Southwest Lancashire Ringing Group where he organized a Barn Owl nest box scheme and study group. He is currently secretary of the Liverpool Ornithologists Club. Back in 1964, he was given a copy of *A Birdwatcher's Anthology* edited by Roger Tory Peterson, which included an extract from Saunders' book *Flashing Wings*. The passage so captured and remained in his imagination that he finally determined to discover all he could about the life and work of its author.

Book Reviews

Book Review Editor's Note: We are continuing to use the current currency codes. Thus Canadian dollars are CAD, U.S. dollars are USD, Euros are EUR, China Yuan Remimbi are CNY, Australian dollars are AUD and so on.

Zoology

Beetles of Eastern North America

By Arthur V. Evans. 2014. Princeton University Press, 41 William Street, Princeton, NJ, USA, 08540-5237. 560 pages, 23.16 USD, Paper.

For those with an inordinate fondness for beetles, finding suitable field guides and reference material has traditionally been a bit of a challenge compared to more charismatic taxa such as butterflies, moths, and (more recently) odonates. My dog-eared 1983 copy of the *Peterson Field Guide to the Beetles of North America* covers 111 families, and despite the 600+ line drawings, there are only 65 colour paintings (this holds true for the 1998 edition as well). More recent field guides to the tiger beetles (Cicindelidae) and jewel beetles (Buprestidae) are welcome and more colourful additions, but leave the majority of beetles treated in a fairly superficial way by more general insect books. On the more technical end of the spectrum, the comprehensive two-volume *American Beetles* by CRC Press (Arnett and Thomas 2000; Arnett *et al.* 2002) are an invaluable reference, but the pair will set you back $280, and the combined 1300+ pages of text may be a bit daunting for the average field naturalist.

Enter Arthur V. Evans' *Beetles of Eastern North America*. According to its preface, the primary goal of the book is to present the beetles of eastern North America in an engaging format that is accessible to the amateur naturalist interested in beetles, while authoritative enough to serve the needs of the professional biologist. Mission accomplished. No longer will the vast majority of Coleoptera languish underappreciated! The 1500+ colour photographs by some of the best insect photographers in North America truly capture the beauty and diversity of our eastern beetle fauna like no other text before it.

Arthur's fantastic new book covers 1409 species and all of the 115 beetle families known from North America east of the Mississippi River. With an 8" x 10" format and 4 lbs of heft, it is not intended for the field and, despite its size, covers only about 10% of the known species for this region. It should however, allow readers to identify to the species level many of the conspicuous beetles they are likely to encounter, and to assign most others to the appropriate genus or family. *Beetles of Eastern North America* reflects the latest taxonomic works, which may confuse some readers where a once-familiar species is reassigned to another group. For example, Ghost Tiger Beetle, long known as *Cicindela lepida* (including in recent field guides) is now referred to as *Ellisoptera lepida*. Fortunately, *Beetles of Eastern North America* includes a taxonomic classification from order through suborder, series, superfamily, etc. down to genus/species. While this appendix may be overkill for some, it can help readers more easily find a reassigned species, and also helps to demonstrate the relationships amongst the diverse beetle groups.

The book opens with about 50 pages of introductory text covering beetle anatomy, behaviour, natural history, and where and when to find beetles. Accompanying photos helpfully demonstrate antennal types, body shapes, tarsal claws, and other features. Arthur has an engaging writing style and it is a much more interesting read than one might expect. Guidance on how to explore the world of beetles is provided, from passive observation and photography to actively collecting and preserving beetles, and even how to rear live beetles and their larvae. The introduction is followed by an illustrated dichotomous key to 68 of the most commonly encountered families in eastern North America. While not as comprehensive as the keys in the two-volume *American Beetles*, they should point the reader in the right direction, especially when used in conjunction with family descriptions from the main body of the book. No one ever said beetle identification was easy!

The main part of the book is organized by family, with a half- to full-page summary of family-level diagnostic characters such as length (mm), shape, color, and distinctive morphological features. Tips are given on how to distinguish each family from other, similar-looking families. A brief overview of the natural history of the group is also provided, as well as notes on suitable collection methods. Finally, the number of species and genera of each family found in the Nearctic and eastern North America are given (if known). This information is very helpful in understanding how diverse the group is, and how many potentially co-occurring species are not illustrated in the book. Similarly helpful is the total number of species in each

genus known from east of the Mississippi River, which is typically provided at the end of the species' accounts.

The species accounts are what set this book apart. There are generally only four species treated per page; this generous layout allows each species' photo to be sufficiently large that the diagnostic features described in the accompany text are often visible. And as a bonus, most of the crisp, vivid photos are of live beetles rather than pinned specimens. One should really use the keys to determine the family, but I would not be surprised if many readers "picture-key" first, and use the text to confirm a beetle's identification. The written descriptions of diagnostic features provided for each species are very useful (if somewhat dry), particularly for small or subtle characters that may not be evident in the photo.

The remainder of each species account consists of concise notes on seasonality, habitat, food preference (for adults and occasionally larvae) and distribution. No range maps are provided (which would be daunting and space-consuming) but the range descriptions help determine whether a species potentially occurs in your general area. Non-native species are also flagged. Surprisingly, Emerald Ash Borer and Asian Longhorned Beetle are not covered in the species accounts but are presented in the introductory section on *Insects as Pests*. More information on the behaviour and natural history would have been welcome for many of the species, but compromises always have to be made when trying to cover as many species as possible in a reasonably-sized tome.

In short, *Beetles of Eastern North America* is an excellent book that will be much loved by field naturalists and entomologists alike, especially given its very modest price.

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Birds of the Kenya's Rift Valley

By Adam S. Kennedy. 2014. Princeton University Press, 41 William Street, Princeton, NJ, USA, 08540-5237. 256 pages, 19.75 USD, Paper.

Birds of Kenya's Rift Valley is the fourth in a series of Princeton University Press WILDGuides by Adam Scott Kennedy, a former safari camp manager and now full-time professional guide. This new field guide focuses on the Kenya's portion of the Rift Valley, which runs through East Africa from the Gulf of Aden south to Mozambique. Kenya's Rift is rich in bird life, with a variety of habitats from soda Lake Magadi and the lush wetlands of Lake Navaisha to the cliffs of Hell's Gate. In particular, Lake Nakuru and Lake Bogoria are famed for their vast flocks of flamingos, which can number in excess of one million birds. Kenya is a renowned location for birding, and this field guide is well suited for visitors of the many national parks and Important Bird Areas of the Rift Valley.

Not surprisingly, there is considerable overlap with Kennedy's two previous bird guides; half of the 320 species covered in the Rift Valley guide are also included in the *Birds of the Masai Mara*. Nonetheless, *Birds of Kenya's Rift Valley* covers a fair bit of new ground since there are approximately 1100 avian species known from Kenya, and the Rift Valley encompasses habitats and areas not found in his Serengeti and Masai Mara guides. For example, Kennedy devotes a full page to Sharpe's Longclaw (*Hemimacronyx sharpei*), an imperilled grassland species found in the Rift Valley highlands. Unfortunately, the guide does not include the similarly endangered Abedare Cisticola (*Cisticola aberdare*), which is also found in the highland grasslands of Mau Narok and the Abedares. Oddly, it also doesn't include such notable species as the Secretary Bird and Kori Bustard. However, the guide does cover 19 species of weavers and no less than ten species of starlings (including the aptly named Superb Starling), which may be surprising to many North Americans used to just one garden variety starling.

Rather than by standard taxonomic order, the guide is arranged into six sections: *Lakes and Marsh*; *Up in the Air*; *Birds of Prey*; *Grasslands and Open Areas*; *Woodland, Scrub and Garden*; and *Nightbirds*. The intent is to help novices more rapidly locate the likely bird species in the guide based on where it is observed, or by groups of birds (raptors, aerial specialists, nocturnal birds) that may range widely over many habitats. This approach has its limitations due to poorly defined or overlapping groups (I must admit I prefer the traditional approach), but may make it easier for beginning birders to identify potential candidates.

What sets this guide apart from other field guides are the 500+ spectacular photographs and impressive artistry of the layout, with truly seamless blending of multiple photos. There are typically 2-3 species per page, with full page accounts for some of the more charismatic or spectacular species such as the Long-tailed Widowbird and Hemprich's Hornbill. The informative and accessible species' accounts have tips on identification and similar species, and touch upon distinctive songs or calls, behaviour, ecology, and other points of interest.

The guide is "intended to be an inspirational, portable, and easy-to-use introduction to the many hundreds of species that have been recorded in the Rift Valley". At 540 g, *Birds of Kenya's Rift Valley* definitely more compact than the more comprehensive *Birds of Kenya and Northern Tanzania* (1000 g, 576 pages, 1114 spp.) by Zimmerman *et al.*, or Stevenson and

Fanshawe's *Birds of East Africa* (1125 g, 602 pages, 1388 spp.). Serious birders will likely want to carry one of these more detailed guides, but Kennedy's new book would serve most safari goers well in Kenya's Rift Valley, and its great photos make it a worthy addition to any birder's bookshelf.

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The Amazing World of Flyingfish

By Steve N. G. Howell. 2014. Princeton University Press, 41 William Street, Princeton, NJ, USA, 08540-5237. 64 pages, 12.95 USD, Cloth.

Many years ago, when I was out on the Gulf Stream off Carolina, I glimpsed a "bird." I spun around, but it had disappeared. Birds just do not disappear, so this was very puzzling. This repeated several times until I realised I was looking at flying fish. Puzzlement then changed to wonder.

I have been fortunate to see these fabulous creatures many times since that day. Standing on the bow of a big cruise ship I noticed the other passengers would ignore birds, but these little fish always caused a stir. There is something magical about flying fish. They appear out of "nowhere" and sparkle in the sun over the deep blue water for a few seconds, before they disappear.

Finding information on these fish has proven difficult. One book I have (A Field Guide to North Atlantic Wildlife, by Proctor and Lynch, Yale University Press) has one page covering five look-alike species. My Field Guide to Atlantic Coast Fishes (By Robins, Ray and Douglass, Houghton Mifflin) covers another seven species. Neither book adds much to my knowledge. Now Steve Howell has written this delightful book. Despite its small size, it contains plenty of useful material. The author acknowledges that the family *Exocoetidae* is poorly known, but he has assembled all the data he can find. The more you learn the more fascinating these fish become. To add to their enchanting appearance they now have the most intriguing names. How can you not perk up for a Leopardwing, a Pacific Necromancer or a Violaceous Rainmaker?

The author admits to taking "a few thousand fuzzy images, ... blank water or water punctuated by only a splash." I too have spent hours trying to get a photograph. Despite there being hundreds of fish actively flying I have way more than my fair share of fish-less ocean water. Therefore it is to Howell's great credit (and his infinite patience) that this book is so beautifully illustrated. Not only are the fish photos technically accurate, many have an ethereal quality. There are photos of some other oceanic "flyers" – rays, dolphins, squid, seals and penguins for comparison. As well there are some nice sequence shots of boobies catching flying fish on the wing.

The Amazing World of Flyingfish (yes it is correctly one word) is amazing. Once I opened it I did not put it down (Perhaps my one complaint is the book is too short. But then one of the author's points is the lack of knowledge about these animals). I now have a strong urge to be back on the bow, looking at the deep blue water, waiting for that mysterious explosion of gossamer and silver. Fish enthusiasts, travelers, naturalists and photographers will love this book, so buy it for friends and family. Most of all buy a copy for yourself.

ROY JOHN

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A Field Guide to the Larger Mammals of Tanzania

By Charles Foley, Lara Foley, Alex Lobora, Daniela De Luca, Maurus Msuha, Tim R. B. Davenport, and Sarah Durant. 2014. Princeton University Press, 41 William Street, Princeton, NJ, USA, 08540-5237. 320 pages, 29.95 USD, Paper.

When I first saw this book I was disappointed by the title "Larger Mammals." I have long been frustrated by African film makers extreme focus on Lions, Leopards, Buffalo, Elephant and Rhino to the exclusion of all else. I have seen three brief videos of the Honey Badger, totalling less than 15 minutes. This is surely one of the most inscrutable mammals of Africa. It is strong, fearless, tireless, tough and courageous. They will defend against any animal, regardless of size. Lions usually lose this fight. Their thick loose skin is impenetrable to bee stings, porcupine quills, and animal bites. They eat anything – insects, frogs, tortoises, rodents, turtles, lizards, snakes, eggs, birds, honey, fruit and vegetables. They are immune to the venom of cobras, mambas and adders. Surely such an astounding beast is worth a few hours of TV time.

When I opened the book I sighed with relief. The Honey Badger was included, as well as many other not-so-large mammals. In fact the authors cover galagos as small as a 12 cm (5 inches). So mongooses, weasels, civets, genets, porcupines and hedgehogs are all incorporated. And all creatures are treated equally. The Lion has a two page coverage, but so does the diminutive White-bellied Hedgehog. The authors cover 135 of the 340 species officially recorded in Tanzania. It does not cover rodents (except three of the big ones), bats or

shrews that make up 60 percent of the mammal list. I did see and photograph one mouse; a Natal Mastomys, *Mastomys natalensis*, that took me two years and multiple emails to identify (by an expert in Belgium). The authors provide a URL for The Field Museum in Chicago (archive.fieldmuseum.org/tanzania/index.html – try it, it is worth a look) that provides an excellent, on-line field guide to all the mammals of Tanzania. Only 16 species of confirmed sea mammals are in this book and the authors state this needs further research, as more species are listed for neighbouring Kenya. Oddly the Field Museum lists 24, but the unconfirmed ones have no detail.

The species accounts are tremendous. The text covering description biology distribution and population is sound. The range maps are large and easy to follow. The authors have added a text box on where to look for each species. This is very useful to all tourists. I do not feel so bad for not seeing a (common) Ground Pangolin when they say you are "very lucky if you do see one."

Each species has at least one and often two or more photographs. They are consistently admirable. Some (Bush Hyrax, White-bellied Hedgehog, Clawless Otter, Cheetah and many antelope) are really cute. The night photos of animals show the eyes as white or red disks that look a little odd. I thought that it would look better if they were photo-shopped, but it is realistic and likely what you with a flashlight.

One animal was quite a surprise; the Kipunji. A close relative of the mangabes, it was the first new monkey to be discovered in 20 years. Only about a thousand of these mammals live in a small corner of Tanzania in a few forest reserves and national parks, making it critically endangered. Its habitat is degraded and fragmented and it suffers from hunting and illegal habitat destruction. No wonder it has a sad look.

There are seven pages of photos that were not labelled so they confused me until I back referenced the pages in the index. They are "Species comparison spreads" – a set of photos with similar species in close proximity. So the reader can compare all the spotted genets and civets, all the mongooses, the antelope and so on. This is so useful for field comparison of look-alike species. When the text notes there are similar species it points you to the correct comparison page.

There is a very important section on the National Parks and major protected areas. Each site has a large photograph overlaid by a locator map and some basic facts. Text boxes list the mammals present with a letter and coloured code indicating their visibility and the chance of seeing one on a two or three day trip. Coupled with the information on the individual species this provides valuable information when planning a trip.

This book is an absolute must for a person going on a safari in Tanzania. It is better than the other mammal guides I own or have seen. It will set you up on where to look. It will help you separate similar species and it will add wonder to your trip. The only other comment I have is that I would like to have this information on Kenya. There is no need to repeat most of the text. A visitor would only need the range maps and the National Park section. Kenya also has a few additional mammals (Grevy's Zebra and White Rhinos for example) so some type of supplement would be nice.

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Reviewers note: While researching the White-tailed Mongoose I was taken aback to find a page devoted to the hunting exploits of a decorated "conservationist." He had arranged to have baited traps set by his safari hosts. Not only did he pot his White-tailed Mongoose, his trusty Remington nailed a Striped Hyena, two Honey Badgers, a Rock Hyrax, a Crested Porcupine, a Black tailed Mongoose and an African Wild Cat. These hardly seem good "trophies" or good to eat.

A Feathered River Across the Sky. The Passenger Pigeon's Flight to Extinction

By Joel Greenberg. 2014. Bloomsbury Publishing Inc., 1385 Broadway, 5th Floor, New York, NY, USA, 10018. 304 pages, 26.00 USD, Cloth.

The Passenger Pigeon is perhaps the most iconic species representing modern extinction and its story has been repeated many times, but only rarely in any detail. The bird's plummet from vast numbers to extinction has often served as a parable illustrating our own species' merciless, Darwinian penchant to convert the rest of nature into ourselves. This year is the 100th since the last Passenger Pigeon expired in a Cincinnati zoo. This centennial is being observed in several events across North America. Joel Greenberg's book is the first detailed account in decades of the Passenger Pigeon's unbelievably rapid descent from billions to none. Greenberg provides meticulous descriptions of our treatment of *Ectopistes migratorius*; our responses to its decline and extinction, our overwhelming ignorance in trying to explain what happened, our unrelenting avarice in "harvesting" it, and our staggeringly short-lived and embarrassingly superficial record of what it was like to have billions of pigeons fly overhead for days at a time, and to have hundreds of millions swoop in to occupy a roost or nesting ground. And what have we learned from this tale of the pigeon of Biblical abundance? I think an accurate answer would be, not much so far, but this book gives us some food for further thought and a basis to consider critically some current approaches to conservation of biodiversity and even our place in nature. Such considerations are appropriate on this centennial of the

Passenger Pigeon's extinction especially given the recognition that we are facing a new so-called 6th global extinction for line which, as is usually assumed to be true for the Passenger Pigeon, we have ourselves to blame. Perhaps new assessment of the conservation implications and lessons of the facts of the Passenger Pigeon's biology and decimation will help us mitigate the current biodiversity crisis; or perhaps it won't.

First, some Passenger Pigeon background, gleaned from this entertaining book. It was a *bona fide* pigeon, closely related to the extant Band-tailed Pigeon (hint to Passenger Pigeon fans; it would be truly helpful in thinking about Passenger Pigeon biology to apply some phylogenetic analysis and direct study of this living bird), and similar to, but slightly larger than our ubiquitous Mourning Dove. It was colourful, a fast, agile flier reputed to zoom along at 60 mph. It produced varied vocalizations, though the descriptions seem somewhat conflicting (screaming, cooing, wooing, bell-like, sleigh bells …), so it is not clear to me what their voices sounded like. The Passenger Pigeon was a typical pigeon in that it built sloppy, rickety nests and fed its squabs pigeon milk ("a curdy substance resembling loose rice pudding") produced by the lining of the crop of both sexes. They usually laid only 1 egg per nest, nested once per year (though this seems uncertain) and probably lived for 10-20 years or more in the wild. They ate almost anything although especially fond of nuts including American Chestnuts, acorns of most species of oaks, and beechnuts all of which to Thoreau's astonishment they swallowed whole. They also ate plants, fruit, invertebrates, seeds, green veggies, grains and more. Their catholic, omnivorous diet is one of their oddly human traits. They occupied most of eastern North America from the Gulf Coast all the way to Hudson Bay (where it is worth noting, there are no nuts) moving about in large flocks of 1000's to millions to billions. These movements were unpredictable, but in part appeared tied to availability of food, especially mast of nut trees. Many times these flocks saved Native and European villages from starvation and, hence, to the immigrants at least, proved the existence of a benign Providence when he showed largesse in sending in the pigeons to feed deprived colonists. In gratitude, "we" eradicated this splendid gift of the Creator.

Greenberg's book is a wealth of interesting factoids, here is a small sample to whet your interest. The largest flock ever "counted" flew over Fort Mississauga, Ontario, Canada in 1860 and numbered 3,717,120,000 (confidence limits undoubtedly huge) individuals. Mayor McCallion in her inaugural term was only mildly thrilled, and expressed concern about the effect of guano on business development and tourism. The main flock zoomed along at "60 miles per hour", took 14 hours to pass and of course blotted out the sun. Smaller flocks continued to fly over for the next several days. The largest nesting "roost" was reported from Wisconsin and "occupied 850 square miles". The total number of birds in North America was thought to be about 5 billion. A large flock (greater than 50,000,000 say), sounded like a "loud rushing roar succeeded by instant darkness", "a noise like the crackling of a fire among dry leaves", "a low pitched hum as they appeared on the horizon …that increased to a mighty throbbing… children screamed, women sought shelter, horses bolted". Audubon recorded a huge flock and mentioned the blocking of the sun, and how the dung fell "not unlike melting flakes of snow", definitely a bravely quaint way to describe being engulfed in a guano storm. The volume of these avian missiles never abated for 3 days, during which of course the sun was eclipsed. Other claims are made (e.g., it outnumbered every other bird species on earth or every other terrestrial vertebrate in North America). All the foregoing is subject to the error of eyewitness testimony and reporting. But an unassailable fact is that less than 50 years after the Ontario super flock, the Passenger Pigeon was extinct in the wild constituting, if nothing else, a tribute to human ingenuity. (See http:http://passengerpigeon.org /index.html (Project Passenger Pigeon), for many more details)

Greenberg spends much of the book chronicling the Passenger Pigeon's abundance, decline and ultimate extinction. He apologizes for the amount of detail he incorporates into the latter topic, and perhaps he should, as it does become a tad tiresome ploughing through pages describing when, where and by whom the last one was lost from the wild, particularly when there seemed to be bigger issues being largely ignored. His excuse is that he wants to be as scholarly as possible, but it is a monotonous litany of shooting pigeon–like birds for the notoriety of bagging the last wild Passenger Pigeon. There is not much of significance to be learned from this, except perhaps that many people crave acclaim, especially when it is as easy as pulling a trigger. The end of wild birds came in about 1902, I think.

I would like to focus on 4 questions that Greenberg discusses less intensively than the awe inspiring abundance and slaughter. What was the ecological "role" of the Passenger Pigeon? How could we know so little about them given their importance and ubiquity? How did 19th century attitudes toward their decline and extinction compare to those we express today about the nature of species at risk? This question is inextricably tied to the big question; what caused the extinction of the Passenger Pigeon, and Greenberg leaves little doubt about his answer; humans. A fourth question, not really covered by Greenberg, is whether we can or should 'de-extinct' the species, or at least some sort of facsimile.

What was the impact of the Passenger Pigeon on North American ecosystems? Greenberg discusses this with interesting possible examples in Chapter 1. The huge numbers of Passenger Pigeon's were enough to

make people wax poetic, express wonder and so on. Some also quailed and were fearful and described consequences that are not generally thought of when we lament the loss of this icon. When the huge flocks whirred, cooed and jingle-belled into an area to roost, their sheer numbers and cumulative mass caused their roosting trees to lose large limbs or to collapse or uproot. In sound and destruction, big flocks were similar to a tornado, leaving destruction everywhere, except tornados don't routinely deposit vast amounts of guano. Soon after the birds arrived the faecal output was over half a metre deep and equivalent to "thousands of wagon loads". Therefore, after the masses moved on not only were all edible fruits, nuts, vegetables, grains, small invertebrates and valuable timber gone, there also was a huge mass of downed woody debris, thousands of pigeon carcasses, remaining trees festooned with excrement, and a choking ground cover of murky indigestibles smelling like a poorly managed factory farm for poultry. The remaining trees cried, the understory died and then it all dried and a lightning bolt converted the forest to ashes, just like modern logging. In many cases, people didn't wait for lightning, but set fire to the roosting/nesting areas, especially if it was a nesting colony, so as to fry the birds and their flightless squabs. They also burned down potential roosts to discourage the arriving flocks from staying and siphoning up local crops. All of this is worth thinking about when one considers how these days a few hundred starlings, crows, rock doves, or geese elicit bitter complaints from the citizenry because of noise, droppings, collisions with aircraft, and occasional direct aggression. What would we do with a few billion pigeons and their whimsical falling flakes?

The impact of these birds on eastern North American ecology must have been prodigious as Greenberg suggests. What that impact was is not at all clear, nor much discussed in the Passenger Pigeon literature, which makes this book interesting in that Greenberg does speculate on some possible effects of the pigeon's passing. We hear a great deal these days about the "functional role" of species X on the "ecosystem" and how ecosystems will change or even collapse if we pull out just one species. But the Passenger Pigeon was not just any species; it was the most abundant terrestrial vertebrate on earth. Couple that with the American Chestnut, population 30 billion and both going extinct within the same century, and it is surprising that any native land forms of life still exist in North America. What was the impact? Well, we don't have native sweet chestnuts to roast nor those gigantic smelly heaps of guano. Greenberg gives some specific hypothetical scenarios resulting from pigeon extinction, one being the rapid decline and now near extinction of the American Burying Beetle (a species worth its own book), and another being the spread of Lyme disease. Lyme carrying ticks are fed largely by *Peromyscus* mice which undergo rapid population increases in high mast years. Greenberg suggests that billions of Passenger Pigeons would stem these mouse peaks and in turn keep tick populations "in check". But on the other hand, mice eat gypsy moths, so Passenger Pigeons competing with mice would lead to moth outbreaks, loss of mast trees and lower Passenger Pigeon numbers. And so such fun speculation goes. The only certainty is that most North Americans have never noticed or thought about these impacts at all.

Well never mind hypothetical ecological roles; how is it that we know so little about the biology and behaviour of Passenger Pigeons beyond the anecdotal and mostly dubious anecdotal at that. At times reading descriptions of the flocks sounding like a "1000 threshing machines…plus 1000 locomotives running full throttle in a covered bridge" , makes one thinks of those low budget movies, called 'invasion of species X'. Let X = Passenger Pigeon. There were lots of pigeons and many people recorded that fact, but there, apparently, serious interest died, except to Hunt them, Kill them, Eat them, Sell them, Market them, Use them as Stoolies, and Marvel at their indestructible abundance. In the 1800's, there were few resources to be wasted studying birds, especially destructive pests. No one investigated their ecology, life history, or behaviour, beyond what was practical knowledge to assist hunting. We can be absolutely certain that no one was trying to conserve or protect them until it was much too late. There was no need, because it was beyond the realm of possibility that they could be exterminated. There are no known photos of Passenger Pigeons in the wild, although there are 2 of wild birds being used as stool pigeons. There is only one known photo of a squab (young pigeon). Even the number of eggs in a clutch was a mystery with the two greatest ornithologists of the time, Alexander Wilson and John James Audubon, feuding over whether it was one or two. Apparently, it didn't occur to them to look. (Greenberg tells us that it was 1, as depicted on the book's cover).

How have attitudes changed since the halcyon days of Passenger Pigeon hordes? This strikes me as a useful question, and one not really addressed by Greenberg. Before I read this book, and more correctly, before I read other sources, I never had much doubt that the extinction of the Passenger Pigeon was caused by humans, not just humans, but humans slaughtering the Passenger Pigeon in market hunting. My experience in the species at risk game has however taught me that when there are large numbers of a species, there are many skeptics who believe that over harvesting cannot extinguish a species. Think of Northern Cod, Bison, Eskimo Curlew, and many others. Even after intense harvest seems to have driven a species to the brink, there are those, particularly those doing the driving, who argue that either it is not at the brink, because they are still abundant, or if they are no longer abundant it was not the harvesters who caused the problem. The cod is a good example of denial from fisher persons,

and the blame being shifted to seals, foreigners, mysterious changes in the water temperature, or that the cod have moved elsewhere (a special case of blaming the victim). Similarly, most 19th, 20th or 21st century accounts of the decline of Passenger Pigeons seem determined to find something more complex than mere slaughter by pigeon hunters. What is delicious about these debates is that the arguments remain so self-servingly constant. In summary the argument goes like this: whatever one thinks, the species is not in danger of extinction, but if it is, then it is not us that caused the problem. Climate change is similar. It is not occurring, the measurements are suspect, they are measuring the wrong things, but if it is true, then it is not man made. I like Greenberg's summary for his bird, "*Homo sapiens* slaughtered the bird methodically and relentlessly. Most everything else is a matter of speculation"

Denial of Abundance

I think there are at least two significant ways that people express skepticism of the Passenger Pigeon story, that are reflected generally today when there is doubt that an "abundant" species is 'truly at risk'. The first and most fundamental is the claim that there never were that many Passenger Pigeons. This skepticism is not surprising given the hyperbolic nature of the descriptions and the paucity of serious effort and ability to quantify numbers. Dismissal of the estimates of billions is easy when one can blame the errors on uneducated, credulous bumpkins from the distant past. And others disparage a few billion, pointing out that there are a lot more chickens today, so what is the big deal. True, there are about 20 billion chickens globally, and 7 billion are slaughtered annually in North America. And come to that, there are over 7 billion of us and we are a much bigger deal than mere pigeons. Greenberg reluctantly reports a more politically correct skepticism expressed recently that the species was naturally uncommon historically because Native Peoples somehow kept their numbers down by hunting and competition. Then when the Europeans arrived and decimated Native populations, the pigeons exploded and for a brief period dominated the skies. There is no support for this odd argument.

In a recent paper in the Proceedings of the National Academy of Sciences (Hung *et al.* 2014; pages 1–6, PNAS Early Edition), a research team reported that the effective population size was much smaller, (on the order of 130,000-24 million), than the 3-5 billion usually indicated. The PNAS team based this astounding conclusion on analysis of the partial genome of 3 Passenger Pigeons from museum collections and from "ecological analysis". The latter led the team to suggest that Passenger Pigeons underwent inherent, frequent, severe fluctuations in population size, and had a population biology like that of lemmings, voles, or even locusts, driven by the periodicity of mast (nuts). So, in a nutshell (sic) population lows, combined with hunting and loss of habitat caused the great demise. The utter lack of similarity between Passenger Pigeon (or Band-tailed Pigeon) and lemming/vole life history, demography, and food habits was never considered in the analyses, or at least not mentioned. No one has reported Passenger Pigeons, or any pigeon or perhaps any bird, with a lemming-like population cycle. It is interesting that they note that *Homo sapiens* has an even smaller effective population size (90 000-170 000) despite its current robust abundance. The team notes that humans achieved this difference by recently starting with a small population and a rapid recent rise, whereas their "ecological analyses" support a Passenger Pigeon history of repeated rapid rises and falls in abundance over the past millions of years. It appears that this model assumes that pigeon carrying capacity depended on annual acorn production. It is true of course that oaks and beech may fluctuate their mast crop dramatically, but not so true that the different species do so neither in synchrony, nor in synchrony with American Chestnut which fluctuated much less than oaks, and which dominated eastern forests until after the demise of the Passenger Pigeon. The notion that Passenger Pigeons underwent fluctuations might be true, but that the evidence and basis for such is sadly lacking or misrepresented in this paper, which has no reference to Greenberg's book or to the known biology of Band-tailed Pigeons, Passenger Pigeons or lemmings.

Denial of Decline

Before the arrival of Europeans, natives hunted the Passenger Pigeon extensively. It is perhaps the most common species in native middens throughout the eastern half of the continent and presumably was a dietary staple. This interaction continued with the early settlers. When the birds came, everyone turned out to stock up on meat, eggs, oil (from the fat squabs), and feathers. They didn't make a much of a dent in their numbers, as far as anyone could tell (but who was counting?) There were not that many people and it was hard to preserve the birds, so the early impacts may not have been large, like the impacts of fishing on the Grand Banks until the factory ships came. In the early days of Native or Settler harvest, cod, bison, Passenger Pigeons and their fellow teeming species were not greatly affected. As the later stages of this tale proceed, we learn that even when the declines became noticed, it was more often than not assumed that the birds were not declining, but merely hiding in remote pigeon secure zones in the far west of the US with the Dalton Gang, or in Argentina, or had crossed the oceans to Europe or Asia. My favourite explanation was presented by Cotton Mather, he of the Salem witch trials, who argued that the birds "migrated to an undiscovered satellite, accompanying the earth at a near distance". One hears similar arguments today about declining species, 'they have moved to where you scientists can't find them', or 'we haven't searched thoroughly enough'.

Denial of Humans as Cause

In the past month, I have watched an interesting video (http://www.youtube.com/watch?v=FpXkA-BY3YE) of a PhD talk suggesting that hunting helped to cause extinction, but loss and fragmentation of habitat was the real culprit. Of course, this doesn't absolve humans from causal agency, but does suggest that we were only guilty of second degree extinction or maybe negligent speciescide. We didn't intend to destroy the species and there was no malice or intent, we were only a little stupid. In this video, the student presents one of her "models" and suggests that this particular model indicates that if in the mid 19th century, conservationists had applied today's IUCN (or COSEWIC) criteria, Passenger Pigeon would have come out Threatened. That was interesting. But her model also showed that hunting was not enough, there had to be a major impact from habitat loss. One of her assumptions built into her models was that hunting pressure decreased with declining Passenger Pigeon numbers, whereas Greenberg's painstaking descriptions lead to the opposite conclusion.

I originally found out about this book through a thought provoking review in the New Yorker (Rosen 2014). In the review, Rosen also suggests that Greenberg is biased in his fingering over harvest as the cause of decline. Rosen makes a confusing, to me at least, argument that hunters were the true conservationists and that rural subsistence hunters in regions of economic hardship often overlap with areas that harbour species at risk. I think this means that if people were to blame, well their sins were justifiable. What Rosen finds less justifiable are "elitists" who conserve vast tracts of wilderness for the public good without a broad consensus. Greenberg doesn't seem to anticipate these sorts of arguments, nor Rosen's expansion on the book's mention of racism in the writings of a scientist who dissected Martha the last Passenger Pigeon. It is of course these digressions by Rosen that made the review interesting.

The Final Days

In this era of climate change and the inevitable deniers, there were Passenger Pigeon extinction/threat /decline deniers. The deniers rested their position on the assertion that humans could not possibly exterminate such an abundant, prolific species, just as we have later argued that we could not possibly decimate Northern Cod, or the myriad other species we have decimated. The story is startling for its monotonous repetitiveness. First, no one thinks about risk at all, then there are feeble concerns expressed that decline is occurring, then denial combined with often bizarre explanations to refute the declines (they have moved, there are still lots of them, there are more than you think, jobs and subsistence food are at stake), then frantic, sometimes futile efforts to "save" the species.

I agree with Rosen that Greenberg is quite ready to blame the less noble properties of humanity for the demise of this splendid creature. But I think Greenberg has a case. After providing a picture of the bird's numbers and habits, he embarks on a seemingly endless account of how they were killed. Nets, bigger nets, shotguns, rifles, pistols, slingshots, air guns, arrows, clubs, fire, saws (cutting down nest trees), cannons and potatoes (this latter only in Orillia, Ontario). In the 19th century, 3 things changed the playing field for the Passenger Pigeon to a near vertical tilt. The telegraph, the railway and the refrigerated rail car. The wandering habits of the Passenger Pigeon now could be tracked via the telegraph, and a huge number of birds could be killed in a short time, preserved and shipped to big city markets for profit. Then ensued relentless and technically improved hunting, the volume of which Greenberg relates with gusto. The story of the fur trade, the feather trade, the timber trade and the fish trade was repeated here. A market was created with little regulation, then the harvest began to reduce the numbers, this led to more hunters per bird than before, especially as more hunters got involved to take advantage of the growing market. The birds helped by being highly social allowing large numbers to be killed on the breeding ground after being located by via a telegraph network. The intense hunting pressure further disrupted breeding and suddenly they were nearly gone, the last big flocks being decimated in final harvest frenzy, and then the trickling remnants hunted casually for dinner or specimens. For the folks who think we couldn't push them to zero, think again, rationally. In other areas, conservation measures and primitive wildlife management saved many once abundant widespread species before it was too late; the goose, the beaver, the fisher, the white pine, and for a while the northern cod, but for the Passenger Pigeon, the bison, the Eskimo Curlew species that were highly clumped at some point in their life history, conservation enlightenment was too late. To illustrate this 'too little too late', Greenberg has several examples of measures to save the Passenger Pigeon that were so late, they seem humourous. Ontario is a typical example. An 1887 Act that protected small birds excluded Passenger Pigeons. A decade later the province gave the pigeon protection, 8 years after the last known specimen was taken in the province. Often the regulations passed in various jurisdictions protected the hunters' rights not the birds' lives. Nothing changes; can anyone say Ontario Snapping Turtle.

Raising the Dead

One can't speculate about the Passenger Pigeon and its collapse without mention of "de-extinction". Rapid advances in genetic tech have beckoned the bio-entrepreneurs out of their basements smelling the colour of money and the lure of fame. TED (Technology, Entertainment, Design) italks abound as speakers ask the rhetorical question, "wouldn't it be fabulous to see extinct species return to life?" And of course, Passenger Pigeon sans guano is one of the most popular candidates. Greenberg spends little space on this, briefly

mentioning cloning in a neutral way. I will be less neutral. De-extinction is in general a foolish idea, and to quote Stuart Pimm, "a spectacular waste of everyone's time". The idea that we can erase the losses of the 1000's of species going extinct right now by resurrecting the lost is ludicrous. Jurassic Park shows what is really involved, hucksterism. In the case of the poor Passenger Pigeon, the current hype suggests using the extant Band-tailed Pigeon as the 'host' for Passenger Pigeon DNA. The irony here is that the Band-tailed Pigeon is itself a species at risk indicating we can't even maintain it much less some chimera cobbled together by biotechnology. Of sad double irony is that while people generally get excited to hear of restoring the glory of abundant Passenger Pigeons, they have no idea what a Band-tailed Pigeon is, and if it goes extinct, I am supremely confident there will be no enthusiasm to de-extinct it. Metaphorically, this effort is like ignoring the wounded in a battle and trying to resurrect the dead. It would be best to wait for the end times then call on the guy who did it 2 millennia ago.

At the end of my Passenger Pigeon odyssey, I offer this thought. It struck me one day that the Passenger Pigeon in its heyday was a lot like us. Think of them and us as sharing a Darwinian background, being molded by overproduction, genetic variation and natural selection. There were 5 billion of them, and there are 7 billion of us. Both are hugely destructive patch disturbers, although we do it on a grossly larger scale befitting our greater intelligence, bulk and numbers. We both have limited genetic variation and much smaller effective population sizes. We are both slow breeders, and long-lived. Both of us are omnivorous and highly social, and we both use Tweets. I won't mention guano again. My point here is not that we are going extinct, but simply that if we think we are a curse on the earth, then so were Passenger Pigeons, even if a more modest one. If we think that their destructiveness and fabled abundance were wonderful, then we can't complain about humans. Nature is such a bitch, and this book will get you thinking about life and biodiversity and us...

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A Sparrowhawk's Lament – How British Breeding Birds of Prey Are Faring

By David Cobham. 2014. Princeton University Press, 41 William Street, Princeton, NJ, USA, 08540-5237. 256 pages, 35.00 USD, Cloth.

There are 15 species of breeding hawks in the UK and I have seen them all, but only 13 in Britain. Exploring the plains of southern England my companion and I spotted a Montague's Harrier. As it was flying away we used the leap-frog technique (one person watching with other running to keep with the bird. When the runner stopped and had the bird in sight the second person became the runner). After a few exchanges we were close to the harrier and I had just caught up with my friend when I saw he was about to sit on an Adder (a venomous snake). I pushed him sideways and in the confusion we lost the bird, but gained a story. As a teenager I was wandering through Scotland with a good friend when we saw a large raptor. We were very excited when we realised it was an Osprey. The next day the reserve warden insisted we took a vow of secrecy to protect the eggs from collectors.

The Osprey epitomises the history of diurnal birds of prey in the British Isles. The over-rich persecuted these birds that interfered with their "sport" and added them to their egg and skin collections, so the Osprey was extirpated by 1916. It did not recolonise until 1954. Even then their recovery was hampered by the effects of organochlorine pesticides and the continual predation by egg collectors. A huge effort by many concerned people have resulted in a current population of 250 pairs. Compare this to an estimated 1500 nests and increasing in Ontario (2001).When travelling with some birders in Assam I was mildly reproached for not showing wild enthusiasm for the daily Osprey sighting. Most summer days I am in the field I see half a dozen or more birds as I live in ideal habitat.

David Cobham describes the status of each of the 15 breeding, diurnal raptors in turn (Red Kite, White tailed Eagle, Western Marsh Harrier, Montagu's Harrier, Hen Harrier, Northern Goshawk

Eurasian Sparrowhawk, Common Buzzard, European Honey Buzzard, Golden Eagle, Osprey, Common Kestrel, Merlin, Eurasian Hobby and Peregrine). His descriptions are detailed, accurate and reveal that he is a careful observer. He often includes large chunks of someone else's text to support his own narrative. He does not need to do this as his writing is most readable. However these inserts are also well written and fit with the flow of information. The author is primarily a film and TV producer and vice-president of the Hawk and Owl Trust. This film-maker "bias" comes through from time to time, most noticeably when he details filming a Goshawks nest in the chapter on Honey Buzzard.

The author's descriptions and his personal anecdotes are charming and a pleasure to read, but the real message of the book is in the history. While all these birds go though many up and downs, seven have become good news stories, while three are still very sad. The remaining five are satisfactory, but need careful monitoring.

Of the good tales the Red Kite is representative. These birds were prevalent in the Middle Ages, but by the 1900s they were only a few pairs in Wales. With the efforts of volunteers and the reintroduction of Swedish birds the author can now report there are now 1,600 pairs in several locations. The Hobby story is similar going from a low of 100 pairs to its current 2800 pairs. The Peregrine had a little different fate. Before World War II there was about 700 pairs, despite being subject to persecution. In the war several hundred were killed to protect military pigeons carrying messages. The population did recovered but plunged again to 400 pairs from effects of DDT. Now the author reports there are 1,500 pairs. The star story is the reintroduction of the White-tailed Eagle. This common bird was extirpated from the UK by 1917. From the release of the first birds in 1975 the population has grown to 64 pairs.

The Golden Eagle has 440 pairs, a stable population size for many years (for comparison the eastern Canadian population is only 200–300 pairs). This is similar to the history of Honey Buzzard and Goshawk. More distressing is the history of the two harriers, Hen and Montagu's.

Although the author reports 630 pairs of Hen Harrier for all the UK it is likely they are almost extirpated in England, although the RSPB reports three nests this year (up from zero in 2013). Raptors are still persecuted despite penalties of a six-month jail sentence or a £5,000 fine. In a 2007 infamous incident two birds were shot by someone at Sandringham, the Queen's estate. A hunting party composed of Prince Harry, a family friend and the estate gamekeeper were questioned, but nobody was prosecuted. In this atmosphere it is not surprising that in the most bird-oriented country (they have over ten times more members per capita in the RSPB than we have in Nature Canada) raptors are still being slaughtered.

David Cobham has written a very understandable biology and history of British birds of prey. It was a pleasure to read the words, but the content was, of necessity, sometimes disturbing. I would recommend this book to all who like birds, particularly raptors. British birders and those who visit (like me) will gain a lot of valuable information. It would make a great present to anyone studying hawks.

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Wildlife of the Caribbean

By Herbert A. Raffaele, and James W. Wiley. 2014. Princeton University Press, 41 William Street, Princeton, NJ, USA, 08540-5237. 304 pages, 19.95 USD, Paper.

There must be a couple of dozen companies offering luxurious Caribbean cruises. Each stops for a day or two on a selection of islands. If you choose not to go on the cruise line's shopping trip, you can explore the some of the wild areas. You can usually find a local birder to help you out.

This guide focuses on 451 species of plants, birds, mammals, herptiles, fish and seashells that you are most likely to see on such a trip. It starts with photographs and descriptions of about 70 widespread plants. The authors have included both native and many introduced, but dramatically beautiful, species. So the reader will find the (African) Tamarind, used to make the much-loved candy balls, an island favourite. Another fruit tree, this time a native, is the Guava famed for its jelly and juice. The traditional Christmas plant, the Poinsettia, has been introduced on many islands, but it is not the familiar pot plant. In the tropical climate it grows to a three to four metre-high tree. Perhaps the most exotic flower is the widespread and dazzling Yellow Bell or Golden Trumpet. Sadly little of the original Caribbean vegetation now exists.

The section on birds, the most extensive part of the guide, follows a conventional field guide style. The illustrations are expertly painted by artists Kristin Williams and Nils Navarro. Generally there are only three to five species per page, giving plenty of room for well-sized depictions. The authors state that there aim was "to include conspicuous and widespread species" so it is reasonable that only 32 percent of the regions birds are covered (179 out of 564). (For a more extensive coverage the ardent birder will need "A Guide to the Birds of the West Indies, by H. Raffeale, Wiley, Garrida, Keith, and J. Raffeale) The description of each species is necessarily brief, but useful. I thought that Status and Range would be the most helpful in the field.

I was delighted to see a section on reptiles and amphibians. It is always much more difficult to find information on these animals. On a typical visit I always see a few lizards or a turtle or two and have a hard time identifying them. I am sure I normally see only the commonest species.

The authors include two drab, freshwater fish and a shrimp. I do not think I paid any attention to looking underwater in streams. Maybe I should. A similar section on marine fish is more extensive, covering 89 species. As most of these are either highly coloured or dramatically large they do claim the tourist's attention. Even without snorkelling I managed to identify 10 of these exotic fish, nine of which are in this book. Oddly missing is the common Caribbean Silversides.

There are smaller sections on marine and land mammals, reptiles and amphibians, butterflies, land crabs and snails. A marine segment, as well as fish, covers

corals, shells and marine invertebrates. These give similar coverage to the larger divisions

So how well do they succeed, considering the author's aim to provide a general nature book of commonly-seen species? I estimate in a couple of trips to the area I saw 85 percent of the birds covered in the book, if I exclude the 68 endemics on islands I did not visit. Because I made a special effort (hiring a local guide) I saw six rarities not in the book (e.g. Grenada Dove, Eurasian Little Egret). I believe I saw approximately 70 percent of the plants depicted. These are very good percentages and suggest the authors have succeeded well.

There are a couple of minor points I noticed. There is no mention of Cayenne Tern and I saw a number of the yellow-billed birds. They are closely related to the Sandwich Tern and are probably the same species. However the taxonomic relationship of these terns is still unresolved. The authors include the St. Vincent Parrot (population about 700 plus) and the nocturnal Cuban Solenodon (population low and unknown). Yet they did not include the iconic Grenada Dove (population over 130).

This small (8 × 5 × ¼ inches) book slips easily into my pants pocket so it is ideal for the travelling naturalist. It covers most of what you will see wandering the Caribbean. The passionate birder will want to take Raffaele *et al.*'s other book mentioned above. While you are en route in your comfortable cabin you should read the introductory section which is a good discussion of the Caribbean's wildlife. The author's give an account of the devastation caused by humans and the efforts being made by some of those humans to retain what is left of this natural heritage.

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BOTANY

Plants of Southern Ontario, Trees, Shrubs, Wildflowers, Grasses, Ferns and Aquatic Plants

By Richard Dickinson, and France Royer. 2014. Lone Pine Publishing, 87 Pender Street East, Vancouver, BC, Canada, V6A 1S9. 527 pages, 29.95 CDN and USD, Paper.

Lone Pine has produced 33 botanical guides mostly covering North America. Five of these specifically cover Ontario: "Trees of Ontario", "Wetland plants of Ontario", "Ontario Wildflowers", "Forest plants of central Ontario", and "Forest plants of northeastern Ontario". There is also the ROM field to wildflowers (Dickinson *et al.* 2004), partly authored by Richard Dickinson. Thus, there are plant groups and regions that are covered more completely in earlier guides by the same publisher and by one of the same authors. For example, Linda Kershaw's "Trees of Ontario" covers 213 species and the guide considered here covers 90. There are also many other guides that cover the various groups in this new book more completely, but it is sometimes convenient to start with a book that has a little of everything. Because it is incomplete however, it does not provide an accurate identification much of the time, although the user may get near to the correct identification and then use more complete books to go further.

The area covered by this guide includes two large ecoregions of southern Ontario, the Southern Deciduous Forest (also known as the Carolinian Zone) and the Great Lakes – St. Lawrence Forest. The plants covered are vascular plants, but although it is implied that they are wild plants, some plants only found in gardens are included such as the Maidenhair Tree (*Gingko biloba*). When a guide is incomplete, the choice of what to include becomes a challenge. It seems best to include what people are most likely to encounter. In this guide the choices have not always been the best. For example, Black Pine, which is not included, is more often seen in plantings and as an escape than Douglas-fir, which is included. The less frequent escape *Euonymus europaeus* is included while the more common, conspicuous, and native *Celastrus scandens* (in the same family) is not.

It is also helpful in an incomplete guide to mention related species that are not covered in depth and there are many places in this guide where that could have been done. On p. 245 under the text on Sundew Family, there is ample space to say that "four species occur in Ontario, one with round leaves, one with linear leaves (both shown here) and two with spoon-shaped leaves one of which has smooth leaf stalks (*D. intermedia*), the other with more or less glandular hairy leaf stalks (*D. anglica*). Likewise for Claytonia there is ample space to refer to the more northern Carolina Spring Beauty (*Claytonia caroliniana*) which has leaves less than eight times as long as broad compared to the Eastern Spring Beauty (*Claytonia virginica*) which has leaves more than eight times as long as broad.

It is not clear what the authority is for the scientific and common names, but for the scientific names at least it appears to be ITIS (Integrated Taxonomic Information System as noted on page 8). For both kinds of names, VASCAN (http://data.canadensys.net/vascan/taxon/6949?lang=en) may be the best choice. Here current scientific names are available and an attempt is made to standardize common names. For example *Spiranthes romazoffiana* is "Hooded Ladies'-tresses"

rather than just "Ladies'-tresses". "*Zigadenus elegans*" is "*Anticlea elegans*". "*Carex eburnea*" is "Bristle-leaved Sedge" rather than "Bristle-leaf Sedge". "Black-grass Rush" should be "Black-grass Rush". The "Dwarf Lake Primrose" should be the "Mistassini Primrose". "Pale Coralroot" should be "Early Coralroot", and etc.

The misidentified photos are disappointing in an identification guide. Following is a list of those I found (in the pre-distribution copy) including page numbers with incorrect name of photo followed by the correct name: 180 right, *Coeloglossum viride* is *Platanthera hyperborea*; 187, *Platanthera hyperborea* is *Platanthera dilatata*; 421, *Elodea canadensis* is *Najas guadalupensis*; 455, *Carex aurea* is *Carex garberi*; 459, *Carex lasiocarpa* is *Carex aquatilis* or *C. stricta*; 475, *Juncus gerardii* is *Juncus secundus*; 486, *Selaginella rupestris* is *Selaginella eclipes*; and 488, *Botrychium multifidum* is *Botrychium lanceolatum*.

There are also mistakes in the descriptions. For example the flowers of Cypripedium orchids have three stamens, one of which is sterile and two of which are reduced but fertile. This guide describes three of them as having a single stamen.

Although this book cannot be recommended without some reservation, and does not come close to the remarkably high standard of quality in the Lone Pine guides for BC produced by Jim Pojar and Andy MacKinnon, it is still a substantial achievement. It includes 528 pages, 760 species, and many impressive photographs (although some are dark). It also provides a useful overview of the wild flora of southern Ontario which includes approx. 3000 species. It is field guide size and stitch-bound with good quality paper. It will stand up well to outdoor use and is good value for the price.

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OTHER

Bird Lady — A Lifelong Love Affair with Birds

By Elizabeth Le Geyt. 2014. Friesen Press Inc., Suite 300 – 852, Fort Street, Victoria, BC, Canada, V8W 1H8. 184 pages, 18.57 CAD, Paper.

Elizabeth Le Geyt is an Ottawa icon. Long before the internet and emails she wrote a column about birds in the Ottawa Citizen's which lasted for 39 years. Using information phoned in by local bird watchers she reported what birds were where and what they were doing. This enabled her readers to make informed decisions on where to go on their own field trips. This gained her an extensive and loyal local following. Unfortunately the column included some bizarre gaffs that irritated the truly passionate birders. Names would get mixed up, for example Broad-shouldered Hawk. Did this mean a Broad-winged Hawk or a Red-shouldered Hawk? Sometimes it would be the numbers that were corrupted. Was there one Snow Bunting with a flock of 250 Snowy Owls or was it really the other way round? So I was not surprised when I read of her joy as a teenager at watching a heronry of Great Blue Herons near her home at Bothwell. The problem is Bothwell is near Glasgow, Scotland, and there is only one record of this North American species in the UK (St Mary's, Isles of Scilly, 7 December 2007). Clearly the author means the Grey Heron (13,000 nests and about 63,000 birds according to the RSPB). The black-and-white photo of a heron's nest that follows, is labelled as Great Blue and I think this is correct. You cannot see the colour of the thighs, but they look grubby, not white.

But this is not a time to pick at the ornithological details in this book. It is the tale of one woman's passion for nature and, in particular, birds. The author recounts her youth in Great Britain and her joy at discovering its many birds. You can follow her journey to adulthood and then her marriage and resultant family. Her husband a Royal Navy officer is posted to Canada; first Halifax then Ottawa. This gives Le Geyt a new group of birds to learn and enjoy.

She is asked to take over the bird column in the Ottawa Citizen. This brings her a whole new coterie of contacts and friends. Her caring nature leads people to bring her orphaned and wounded wildlife. Eventually she forms a liaison with the Wild Bird Care Centre where injured animals are treated and rehabilitated and released back into a typical habitat. It is questionable whether a hand-reared creature placed in the wild would fare well. If the habitat is ideal it likely has a resident occupier, who will drive any newcomer away. Eventually it will be driven to poor habitat where it will be vulnerable to starvation and predation. However the process of caring for the distressed and helpless creatures has a powerful message to the untutored public. Le Geyt and her friends have raised the awareness of the plight of wildlife and the environment and much of this has been achieved through their rescue efforts.

The author gives a concise portrayal of the important wildlife areas of the Ottawa area. She describes her adventures with Jacko, an African Grey Parrot, Joey the Rock Pigeon; and Rattles the kingfisher. She also reports on trips she took to South Africa, Mexico, Costa Rica, Trinidad, Arizona and her return to Great Britain.

Elizabeth Le Geyt is a good writer who uses a light, breezy style to bring the reader into her passion. Her tales are told with warmth and humour. I really enjoyed learning of her childhood and comparing it to my own. The wonder she shows at seeing her first Canadian birds is something else I can share. When she describes the exploits of Jacko, Joey and Rattles her writing reflects her own warm and kindly nature. Her journeys to other countries again reminds me of my own travels.

I think all those readers who followed Le Geyt's column will delight in this book. Any one who loves nature will enjoy this light-hearted book. The reader will feel relaxed and uplifted with every chapter, so perhaps even non-naturalists should buy a copy — it will improve their environmental awareness. This delightful book is a remarkable achievement for a woman who is over 100 years old.

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The Dismal State of the Great Lakes

By James P. Ludwig. 2013. Xlibris. Orders@Xlibris.com. Telephone 1-888-795-4274. 273 pages. Paperback 19.99 USD; hardcover 29.99 USD; e-book 3.99 USD. Printed on demand.

The Laurentian Great Lakes of North America contain 18 percent of the planet's fresh surface water and 90 percent of the United States' supply. The Great Lakes region has been the major manufacturing hub of North America, and has supplied vast quantities of timber and minerals, particularly iron ore, to the world's markets. Today, agriculture, recreation and tourism, fishing, and shipping are the important industries. The Boundary Waters Treaty of 1909 between the governments of Canada and the United States established an International Joint Commission and mechanisms for resolving any disputes over waters bordering the two countries, as they pertained to their use for domestic and sanitary purposes, navigation, power, and irrigation. The Great Lakes Water Quality Agreement of 1972/78 committed the Parties to cooperation in the restoration and maintenance of the chemical, physical, and biological integrity of the waters of the Great Lakes Ecosystem. These legislative tools attest to the tremendous importance of the Great Lakes to Canada and the United States and to planet Earth. Unfortunately, the scientific findings documenting the demise of the Great Lakes, and the political failure to address their implications are not well-known outside the Great Lakes community. *The Dismal State of the Great Lakes* is James P. Ludwig's attempt to remedy that by detailing his personal and professional journey in studying the extensive damage that has been done to the Great Lakes over his lifetime, the once-promising but eventual political failure to restore them, and his analysis of why they happened and how we might fix the mess.

This is a book written by an ageing, angry man with a fire in his belly for justice and a deep love for these great "sweetwater seas." It is "a call to debate the possible paths to effective change and to reignite the fires of public involvement." This is a book with an important message.

The Ludwig family have documented the biological changes in the Great Lakes for over 70 years. Jim Ludwig's father and uncle, both physicians, were the first of two generations of admittedly "compulsive bird banders," who each year visited the colonies of cormorants, gulls and terns to place aluminum bands on the young birds. On these occasions they recorded the catastrophic effects of a succession of chemicals and invasive species. Trained in science, they kept good records, understood the implications of what they were seeing, and raised the appropriate "red flags." Jim Ludwig was awarded a PhD from the University of Michigan in 1968 for his thesis entitled "Dynamics of Ring-billed Gull and Caspian Tern populations of the Great Lakes." He founded Ecological Research Services, a small consulting firm, in 1969. Glenn Fox (GAF), who also devoted his career to the study of fish-eating birds in the Great Lakes, has collaborated with Jim Ludwig directly and indirectly, in research projects. Stuart Houston (CSH), a physician and compulsive bird bander, has corresponded occasionally with the Ludwigs, father and son, since the 1950s.

Ludwig's story consists of several threads. One deals with the biological information; alien species, eutrophication, algal toxicity, botulism, changes in the nature, size, and nutritional quality of the food base, and the effects of toxic chemicals on the health, reproduction, and survival of fish-eating birds and mammals, including humans. Another deals with the complex and on-going contamination by toxic chemicals; their detection, identification, sources and environmental behaviour, and our efforts to control their release. A third is the history of the Great Lakes fishery, its management, and the conflicted culture of fisheries managers. The final thread is the socio-political history surrounding the Great Lakes Water Quality Agreement and the International Joint Commission, the successes and failures of numerous collective actions and Ludwig's interpretation of what went wrong. He suggests how to get it right in the future.

Alien species. The Great Lakes have been invaded by numerous alien species. The sea lamprey, which infested Lake Ontario via the St. Lawrence River, and the upper Great Lakes with the completion of the Welland Ship Canal in 1932, greatly impacted Lake Trout

(and later introduced salmon) stocks. The Alewife, a small herring, invaded the Great Lakes by a similar route and became superabundant. It suffered periodic die-offs in response to sudden changes in water temperature; extraordinary numbers of their dead and dying bodies were cast up on beaches. Alewives became a major food item for Ring-billed Gulls, whose populations increased tenfold to a million birds. Zebra and Quagga Mussels, Round Gobies, and the Spiny Water Flea were among many alien species introduced in ballast water of ships from the Baltic Sea. Today, the vast populations of these mussels filter out much of the phytoplankton, altering energy transfer in the food web; moribund gobies are eaten by loons and cormorants who then die from ingesting botulism toxin concentrated within the gobies.

Eggshell thinning, the first of many health effects observed in fish-eating birds. Bald Eagle productivity dropped drastically due to eggshell thinning caused by DDE which was widely used by the mid-1940s. The effects persisted from 1955 until a decade after widespread use of DDT was banned in 1972. In 1972, a high percentage of cormorant eggs failed to hatch. None of the eggs in the second clutch hatched that year. This was attributed to severe DDE-induced eggshell thinning [cormorants incubate by standing on their eggs]. Cormorants and bald eagles were the most affected by DDT, gulls the least.

Crossed bills in cormorant chicks warn of developmental toxins in Great Lakes fish. In June 1983, on Little Gull Island in northern Green Bay, Ludwig found 5 of 460 cormorant chicks had crossed bills, the first he had seen, an unusually high incidence of a developmental defect. By June 1988, he had collected 41 more cross-billed cormorant chicks, but only 1 from Canadian colonies. He also saw numerous chicks with eye, leg and hip deformities. These findings suggested that biologically significant amounts of developmental toxins were present in Great Lakes food webs. Intensive collaborative studies involving teams of analytical chemists and toxicologists from Michigan State University, Ehime University in Japan, a teratologist and biologists from the U.S. Fish and Wildlife Service and the Canadian Wildlife Service suggested that nearly 90% of the variability in egg viability among colonies was explained by TCDD-EQs (tetrachlorodibenzo-p-dioxin equivalents) in the eggs alone. The Michigan Department of Natural Resources initially encouraged these studies and provided the funding for the work in 1986-88. However, the arrival of a new director and strong criticism from MDNR biologists who were furious over findings released to the public which could reduce fishing license sales resulted in withdrawal of MDNR support. Fortunately, Dow Chemical and Upjohn Pharmaceuticals (two companies who used, made, and discharged a wide variety of chemicals), the McGregor Foundation of Detroit, and Consumers Power Corp stepped up to provide finances to complete the studies, which provided very strong cause-effect linkages between these biological effects and dioxin-like synthetic chemicals.

Cosmos the Cormorant, poster child for toxic chemical regulation. Much public interest and political support was generated by Cosmos, a cormorant chick with a severely crossed bill that Ludwig rescued from an island in northern Lake Michigan in June 1988. Ludwig made himself a promise that he "would do everything possible to keep Cosmos alive, and he would handle the public relations for the movement to ban toxic chemicals and clean-up Great Lakes' Areas of Concern with high contamination." Cosmos made 16 TV appearances in the United States and Japan and testified by her presence in numerous state and federal legislative committees, and accompanied Ludwig on 27 evening presentations to environmental and teachers groups in five of the Great Lakes states. Ludwig writes "I think it safe to claim Cosmos in her single short year of life did more to propel the issue of toxic chemicals to the forefront of political agendas in Michigan and Wisconsin than all the other environmental activists and scientists were able to achieve through lobbying or explaining their findings." Cosmos's legacy lives on in Japan where she has become the symbol of the dangers of unregulated toxic chemical use. She was the cover image on the fifth grade textbook on pollution and climate change that is used in all Japanese public schools.

Bird Banding reveals population level impacts of chemical contaminants. Ludwig's family began banding Caspian Terns and other colonial waterbirds in 1922 and continued to do so until 1995. Jim periodically trapped nesting adults in some of these same colonies 1966–1992. By 2008, he had amassed 7000 encounter records of Caspian Terns banded as chicks in Great Lakes colonies. This immense and unique data set has proven very useful. As early as 1971, he found that nearly half of adults in Lake Michigan colonies were hatched in Canadian colonies which was not the case in 1966 and 1967. When Ludwig analyzed the 7000 encounters, he found, that relative to birds raised in Canadian colonies, survival to adult age in the most contaminated colonies in Saginaw Bay and Green Bay was 20% and 30%, respectively, while that of colonies with intermediate contamination in northern Lake Michigan was 59%. This pattern in relative survival to breeding age was almost identical to that of relative immunocompetence in chicks of this species that Keith Grasman, a Ph D student from Virginia Tech measured in these same colonies 1989–1992. In Saginaw and Green Bay colonies the immunocompetence of chicks was less than 50% of that in the cleaner Canadian colonies in Lakes Huron and Superior and was inversely correlated with TCDD-EQs in the eggs from these colonies. Caspian Terns banded as nesting adults in Canadian colonies survived twice as long as adults banded in Saginaw Bay colonies, 5 years longer than

those from Green Bay colonies, and 4.2 years longer than those from northern Lake Michigan colonies. Previous investigations had found a significant negative correlation between recruitment of terns in these colonies and circulating blood concentrations of total PCBs. PCB concentrations in the blood of adults from the Canadian colonies were half those in blood of terns nesting in Saginaw and Green Bay colonies. It is not surprising that Ludwig makes a strong pitch for long-term studies and adequate funding for investigators.

Toxic chemical contamination. Ludwig does a good job of describing and explaining the universal role of energy transfer and bioaccumulation in natural systems and how trace amounts of synthetic chemicals are similarly transferred and bio-accumulated to toxic concentrations. A great many persistent toxic chemicals pollute the waters of the Great Lakes. Mercury, polycyclic aromatic hydrocarbons, the insecticide DDT, hexachlorobenzene, and the polychlorinated biphenyls (PCBs) and dioxins have probably been the most important. Like important amino acids and hormones in animal bodies, the most prominent synthetic toxic compounds have a backbone of six carbon biphenyl rings. Synthetic compounds containing two biphenyl rings to which chlorine, fluorine, or bromine are attached to some of their carbon atoms are the compounds that have caused the greatest damage. Their toxicity varies by a million-fold with the number and position of the halogen constituent on the biphenyl rings. The most potent of these compounds is 2,3,7,8-tetrachlorodibenzo-*para*-dioxin (TCDD). Toxicologists rate the toxicity of other halogenated aromatic hydrocarbons relative to TCDD and express the total toxicity of extracts from tissues and environmental media as TCDD-Equivalents (TCDD-EQs). They act via a specific receptor present in cells: the aryl hydrocarbon (AH) receptor, a transcription factor involved in expression of genes. TCDD-like compounds alter thyroid function and other metabolic processes, cause birth defects and permanent neurological damage in embryos and young animals, are endocrine disrupters, and immunomodulators. Some or all of these effects have been seen in fish, amphibians, reptiles, birds, and mammals including humans. Much of what is known about the environmental effects and dangers of these chemicals has been learned from investigations conducted in the Great Lakes. Several studies have shown effects on motor and behavioural development of infants and lower intelligence quotients of older children of mothers who ate significant amounts of fish from Lakes Michigan and Ontario. The severity of these effects was associated with the mother's PCB exposure.

The Fishery. Throughout their history, the Great Lakes have been important for fish, and to people who depend on them for food, subsistence, income, and recreation. The relative importance of these activities has varied over time. Unsustainable commercial fishing activity decimated the Lake Sturgeon in the 1880s and the Blue Pike in the 1960s. Atlantic Salmon populations in Lake Ontario were also hurt by overfishing. However, although not accepted by many fisheries biologists, there is clear scientific evidence that Lake Trout populations in Lake Ontario and probably elsewhere in the Great Lakes were greatly affected by TCDD-like chemical contamination. Research published in 2003 showed that the extirpation of native Lake Trout from Lake Ontario during the three decades following WWII was the result of TCDD-like contaminants which killed all embryos of the wild Lake Trout for over 20 years, extinguishing the stock. Today the dominant salmonids in the Great Lakes are various species of introduced Pacific salmon whose populations are maintained with hatchery stock, and are harvested mainly by sport fisherman. Recent estimates place the value of the sport fishing industry to the Great Lakes economy at 4 billion dollars, and the commercial fishery at 1 billion dollars. There is a clear conflict between natural resource managers who benefit from the sale of fishing licenses and public health authorities who are issuing consumption advisories for fish taken in badly contaminated locations around the Great Lakes. Ludwig believes this conflict is one of the reasons that funding for health effects research and monitoring disappeared, and that a culture of "good news only" ("One must never allow bad news to be publicized!") pervades governments around the Great Lakes today.

The greatest legacy of the Boundary Waters Act of 1909 was the creation of the binational International Joint Commission. The Great Lakes Water Quality Agreement of 1972 committed the Parties to cooperation in the restoration and maintenance of the chemical, physical, and biological integrity of the waters of the Great Lakes Ecosystem. For many years the Commissioners, Parties, and Great Lakes citizens worked hard at achieving those objectives, supported by sound science. However, as public concern increased concerning the health effects of persistent toxic substances, the Parties adopted a defensive position, limiting support for research, monitoring and information dissemination. The International Commission's work was subverted. The objective of virtual elimination of persistent toxic substances was regarded as too expensive by successive governments. Hence their policy focus became a vague, multi-causal, "Ecosystem Approach" which redirected funding and concern away from the study of biological effects, remediation, and science-based policy. The result was a series of regulatory blunders, avoidance of assigned duties, and far too much reliance on use of models and simplistic indicators. No surprisingly, the chemicals of concern and their biological effects persist.

Ludwig's book includes his 1995 editorial in the *Journal of Great Lakes Research* (21:159-160), suggesting that the Science Advisory Board of the International Joint Commission had degenerated into a

means to achieve a politically acceptable consensus. What else has gone wrong in government? As Al Gore said, "The private foxes have been put in charge of the public hen houses." In the USA, the US Environmental Protection Agency, created by Richard Nixon in late 1970 and the Department of the Interior have been "largely emasculated," "intellectually corrupted," and "a form of ecological insanity" according to Ludwig. No one and no agency is responsible for management of the whole resource of the Great Lakes ecosystem; there is a hodge-podge of funding, too many barriers to effective communication, incredible redundancy, very poor accountability, and no clear place for the public to redress grievances. Sound, evidence-based science is required but no longer encouraged or supported. Although the lifetime and multi-generational needs of the commonweal are far more important than money accumulation by the individual and corporations, this is incompatible with the neoliberal politicians of today.

Jim Ludwig is an "insider" who suggests how to rectify the current disastrous situation. Society needs wise and informed advocates with ecological knowledge, who are committed to change. We need to discard free-market policies of neglect, passivity and deception, and commit to good water quality by restoring powers of the original Great Lakes Water Quality Agreement and the International Joint Commission. Critical analyses must no longer be suppressed and ignored. If only Ludwig's facts and insight would direct the authorities to appropriate action!

The Dismal State is correctly titled, but is a disappointment in several ways. Its importance deserved a University press, careful external editing, better organisation, more headings, an index, a more complete list of acronyms, and a better binding for the paperback version (twenty two-sided pages of CSH's paperback review copy have already come loose). Sadly, Ludwig's writing will seem too personal and too political for some tastes. However, he has accurately documented what has gone wrong. If nothing else, his testimony will remain as a valid historical record.

The Dismal State of the Great Lakes has not yet achieved the distribution it deserves. I offer a promising possibility for consideration: that each regional nature club invest a hundred dollars to help the Great Lakes' future. Each could order e-book copies for five of its members to pass around and donate one copy of the permanent hardcover version to the adjacent high school, college or University library. We are doing the latter. Ludwig's valuable information assuredly deserves to be more widely distributed.

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NEW TITLES

Prepared by Roy John

† Available for review * Assigned
Currency Codes – CAD Canadian Dollars, USD U.S. Dollars, EUR Euros, AUD Australian Dollars.

ZOOLOGY

*** North American Amphibians: Distribution and Diversity.** Edited by David M. Green, Linda A. Weir, Gary S. Casper, and Michael Lannoo. 2014. California-Princeton Fulfillment Services, 1445 Lower Ferry Road, Ewing, NJ, USA, 08618. 352 pages, 75.00 USD, Cloth.

Dam Builders: The Natural History of Beavers and their Ponds. By Michael Runtz. 2014. Fitzhenry & Whiteside Limited, 195 Allstate Parkway, Markham, ON, Canada, L3R 4T8. 254 pages, 35.00 CAD, Cloth.

The Bee: A Natural History. By Noah Wilson-Rich. 2014. Princeton University Press, 41 William Street, Princeton, NJ, USA, 08540-5237. 224 pages, 27.95 USD, Cloth.

Phillipps' Field Guide to the Birds of Borneo: Sabah, Sarawak, Brunei, and Kalimantan (3rd Edition). By Quentin Phillipps, and Karen Phillipps. 2014. Princeton University Press, 41 William Street, Princeton, NJ, USA, 08540-5237. 384 pages, 35.00 USD, Paper.

American Birding Association Field Guide to Birds of Colorado. By Ted Floyd. 2014. Scott & Nix, Inc., 150 West 28th Street, Suite 1900, New York, NY, USA, 10001. 320 pages, 19.93 USD, Paper.

American Birding Association Field Guide to Birds of New Jersey. By Rick Wright. 2014. Scott & Nix, Inc., 150 West 28th Street, Suite 1900, New York, NY, USA, 10001. 368 pages, 24.95 USD, Paper.

Common Birds of Nunavut. By Mark Mallory. 2014. Inhabit Media Inc., P.O. Box 11125, Iqaluit, NU, Canada, X0A 1H0. 32 pages, 19.95 CAD, Paper.

*** Illustrated Checklist of the Birds of the World – Volume 1 (Non-passerines).** By Josep del Hoyo, Nigel Collar, David Christie, Andrew Elliott, and Lincoln Fishpool. 2014. HBW and BirdLife International, Lynx Edicions, Montseny, 8, 08193 Bellaterra, Barcelona, Spain. 904 pages, 185.00 EUR, Cloth.

The World of Birds. By Jonathan Elphick. 2014. Firefly Books Ltd., 50 Staples Avenue, Unit 1, Richmond Hill, ON, Canada, L4B 0A7. 640 pages, 75.00 CAD, Cloth.

Prairie Dog Empire: A Saga of the Shortgrass Prairie. By Paul A. Johnsgard. 2014. Barnes and Noble, Inc., P.O. Box 111, Lyndhurst, NJ, USA, 07071. 243 pages, 22.95 USD, Cloth.

*** The Amazing World of Flyingfish.** By Steve N. G. Howell. 2014. Princeton University Press, 41 William Street, Princeton, NJ, USA, 08540-5237. 64 pages, 12.95 USD, Cloth.

The Illustrated Handbook of Fossils: A Practical Directory and Identification Aid to More Than 300 Plant and Animal Fossils. By Steve Parker. 2014. Barnes and Noble, Inc., P.O. Box 111, Lyndhurst, NJ, USA, 07071. 160 pages, 18.99 CAD, Cloth.

In Search of Lost Frogs. By Robin Moore. 2014. Firefly Books Ltd., 50 Staples Avenue, Unit 1, Richmond Hill, ON, Canada, L4B 0A7. 256 pages, 35.00 CAD, Cloth.

Hummingbirds. By Ronald Orenstein. 2014. Firefly Books Ltd., 50 Staples Avenue, Unit 1, Richmond Hill, ON, Canada, L4B 0A7. 256 pages, 35.00 CAD, Cloth.

*** Life on the Rocks – A Portrait of the American Mountain Goat.** By Bruce Smith. 2014. University Press of Colorado, 5589 Arapahoe Ave., Suite 206C, Boulder, CO, USA, 80303. 176 pages, 34.95 USD, Cloth.

Hoofed Mammals of British Columbia – 2nd Edition. By David Shackleton. 2013. Royal BC Museum, 675 Belleville Street, Victoria, BC, Canada, V8W 9W2. 272 pages, 25.95 CAD, Paper.

***A Field Guide to the Larger Mammals of Tanzania.** By Charles Foley, Lara Foley, Alex Lobora, Daniela De Luca, Maurus Msuha, Tim R. B. Davenport, and Sarah Durant. 2014. Princeton University Press, 41 William Street, Princeton, NJ, USA, 08540-5237. 320 pages, 29.95 USD, Paper.

Marmot Biology – Sociality, Individual Fitness, and Population Dynamics. By Kenneth B. Armitage. 2014. Cambridge University Press, Shaftesbury Road, Cambridge, UK, CB2 8BS. 410 pages, 120 USD, Cloth.

The Passenger Pigeon. By Errol Fuller. 2014. Princeton University Press, 41 William Street, Princeton, NJ, USA, 08540-5237. 184 pages, 29.95 USD, Cloth.

* **A Feathered River Across the Sky: The Passenger Pigeon's Flight to Extinction.** By Joel Greenberg. 2014. Bloomsbury Publishing Inc., 1385 Broadway, 5th Floor, New York, NY, USA, 10018. 304 pages, 26.00 USD, Cloth.

***The Fish in the Forest – Salmon and the Web of Life.** By Dale Stokes. 2014. University of California Press, 155 Grand Avenue, Suite 400, Oakland, CA, USA, 94612–3758. 172 pages, 29.95 USD, Cloth.

Creatures of the Deep – In Search of the Sea's "Monsters" and the World They Live In – 2nd Edition. By Erich Hoyt. Firefly Books Ltd., 50 Staples Avenue, Unit 1, Richmond Hill, ON, Canada, L4B 0A7. 208 pages, 39.95 CAD, Cloth.

Shrewdunnit: The Nature Files. By Conor Jameson. 2014. Pelagic Publishing Ltd., PO Box 725, Exeter, UK, EX1 9QU. 300 pages, 14.99 GBP, Cloth.

* **A Sparrowhawk's Lament – How British Breeding Birds of Prey Are Faring.** By David Cobham. 2014. Princeton University Press, 41 William Street, Princeton, NJ, USA, 08540-5237. 256 pages, 35.00 USD, Cloth.

Guide to Minnesota's Reptiles and Amphibians. By John J. Moriarty, and Carol D. Hall. 2014. University of Minnesota Press, Suite 290, 111 Third Avenue South, Minneapolis, MN, USA, 55401. 400 pages, 39.95 CAD, Cloth.

Biology and Conservation of North American Tortoises. By D. Rostal, E. McCoy, and H. Mushinsky. 2014. John Hopkins University Press, 2715 N. Charles Street, Baltimore, MD, USA, 21218. 190 pages, 69.95 USD, Cloth.

The Trilobite Book: A Visual Journey. By Riccardo Levi-setti. 2014. The University of Chicago Press, 1427 East 60th Street, Chicago, IL, USA, 60637. 288 pages, 49.30 CAD, Cloth.

Woodpeckers of the World – A Photographic Guide. By Gerard Gorman. 2014. Firefly Books Ltd., 50 Staples Avenue, Unit 1, Richmond Hill, ON, Canada, L4B 0A7. 528 pages, 49.95 CAD, Cloth.

BOTANY

Carnivorous Plants of Australia Magnum Opus Volume 1. By Allen Lowrie. 2014. 61 Redfern Natural History Productions, Lake Drive, Hamworthy, Poole, Dorset, UK, BH15 4LR. 458 pages, 34.99 GBP, Cloth.

Carnivorous Plants of Australia Magnum Opus Volume 2. By Allen Lowrie. 2014. 61 Redfern Natural History Productions, Lake Drive, Hamworthy, Poole, Dorset, UK, BH15 4LR. 450 pages, 34.99 GBP, Cloth.

Carnivorous Plants of Australia Magnum Opus Volume 3. By Allen Lowrie. 2014. 61 Redfern Natural History Productions, Lake Drive, Hamworthy, Poole, Dorset, UK, BH15 4LR. 463 pages, 34.99 GBP, Cloth.

A Great Lakes Wetland Flora: A Complete Guide to the Wetland and Aquatic Plants of the Midwest. By Steve W. Chadde. 2012. Barnes and Noble, Inc., P.O. Box 111, Lyndhurst, NJ, USA, 07071. 692 pages, 44.86 CAD, Paper.

* **Plantes de milieux Humides et De Bord De Mer – du Québec et Des Maritimes.** By Martine Lapointe. 2014. Éditions Michel Quintin, 4770, rue Foster, Waterloo, QC, Canada, J0E 2N0. 456 pages, 34.95 CAD, Paper.

* **Plants of Southern Ontario.** By France Royer, and Richard Dickinson. 2014. Lone Pine Publishing, 87 East Pender Street, Vancouver, BC, Canada, V5A 1S9. 528 pages, 19.76 CAD, Paper.

* **Trees of Eastern North America.** By Gil Nelson, Christopher J. Earle, and Richard Spellenberg. 2014. Princeton University Press, 41 William Street, Princeton, NJ, USA, 08540-5237. 720 pages, 29.95 USD, Paper, 65.00 USD, Cloth.

* **Trees of Western North America.** By Richard Spellenberg, Christopher J. Earle, and Gil Nelson. 2014. Princeton University Press, 41 William Street, Princeton, NJ, USA, 08540-5237. 560 pages, 29.95 USD, Paper, 60.00 USD, Cloth.

The Glory of the Tree – An Illustrated History. By Noel Kingsbury. Firefly Books Ltd., 50 Staples Avenue, Unit 1, Richmond Hill, ON, Canada, L4B 0A7. 288 pages, 39.95 CAD, Cloth.

Common Mosses of the Northeast and Appalachians. By Karl B. McKnight, Joseph R. Rohrer, Kirsten McKnight Ward, and Warren J. Perdrizet. 2013. Princeton University Press, 41 William Street, Princeton, NJ, USA, 08540-5237. 392 pages, 24.95 CAD, Paper.

Other

Algonquin Park: A Portrait – The landscape, wildlife and ecology of an iconic Canadian treasure. By Jan and Martin Rinik. 2014. Formac Publishing, 5502 Atlantic Street, Halifax, NS, Canada, B3H 1G4. 216 pages, 34.95 CAD, Cloth.

Essentials of Conservation Biology – 6th Edition. By Richard Primack. 2014. Sinauer Associates, Inc., 23 Plumtree Road, P.O. Box 407, Sunderland, MA, USA, 01375-0407. 603 pages, 94.95 USD, Cloth.

* **Bird Lady — A Lifelong Love Affair with Birds.** By Elizabeth Le Geyt. 2014. Friesen Press Inc., Suite 300 – 852, Fort Street, Victoria, BC, Canada, V8W 1H8. 184 pages, 18.57 CAD, Paper.

Botanical Illustrators Handbook. By Sally Pinhey. The Crowood Press, The Stable Block, Crowood Lane, Ramsbury, Wiltshire, UK, SN8 2HR. 128 pages, 16.99 GBP, Paper.

* **Ancient Pathways, Ancestral Knowledge – Ethnobotany and Ecological Wisdom of Indigenous Peoples of Northwestern North America.** By Nancy J. Turner. 2014. McGill-Queen's University Press, 1010 Sherbrooke West, Suite 1720, Montreal, QC, Canada, H3A 2R7. 1056 pages, 100.00 CAD, Cloth.

Extinction and Evolution – What Fossils Reveal About the History of Life. By Niles Eldredge. Firefly Books Ltd., 50 Staples Avenue, Unit 1, Richmond Hill, ON, Canada, L4B 0A7. 256 pages, 45.00 CAD, Cloth.

Running Silver: Restoring Atlantic Rivers and their Great Fish Migrations. By John Waldman. 2013. Lyons Press (Globe Pequot Press), 246 Goose Lane, P.O. Box 480, Guilford, CT, USA, 06437. 284 pages, 29.95 USD, Paper.

Tales from Gombe. By Anup Shah, and Fiona Rogers. 2014. Firefly Books Ltd., 50 Staples Avenue, Unit 1, Richmond Hill, ON, Canada, L4B 0A7. 320 pages, 69.95 CAD, Cloth.

Drawing and Painting Insects. By Andrew Tyzack. 2014. The Crowood Press, The Stable Block, Crowood Lane, Ramsbury, Wiltshire, UK, SN8 2HR. 192 pages, 32.95 CAD, Cloth.

Wildlife Photographer of the Year – 50 Years – How Wildlife Photography Became Art. Edited by Rosamund Kidman Cox. 2014. Firefly Books Ltd., 50 Staples Avenue, Unit 1, Richmond Hill, ON, Canada, L4B 0A7. 256 pages, 49.95 CAD, Cloth.

* **Wallace, Darwin, and the Origin of Species.** By James T. Costa. 2014. Harvard University Press, 79 Garden Street, Cambridge, MA, USA, 02138. 352 pages, 39.95 USD, Cloth.

Juvenile

Saving Turtles – A Kid's Guide to Helping Endangered Creatures. By Sue Carstairs. 2014. Firefly Books Ltd., 50 Staples Avenue, Unit 1, Richmond Hill, ON, Canada, L4B 0A7. 64 pages, 9.95 CAD, Paper.

Weird Birds. By Chris Earley. 2014. Firefly Books Ltd., 50 Staples Avenue, Unit 1, Richmond Hill, ON, Canada, L4B 0A7. 64 pages, 9.95 CAD, Paper.

Weird Frogs. By Chris Earley. 2014. Firefly Books Ltd., 50 Staples Avenue, Unit 1, Richmond Hill, ON, Canada, L4B 0A7. 64 pages, 9.95 CAD, Paper.

Monsters of the Deep. By Camilla de la Bédoyère. 2014. Firefly Books Ltd., 50 Staples Avenue, Unit 1, Richmond Hill, ON, Canada, L4B 0A7. 80 pages, 9.95 CAD, Paper.

Creatures of the Night. By Camilla de la Bédoyère. 2014. Firefly Books Ltd., 50 Staples Avenue, Unit 1, Richmond Hill, ON, Canada, L4B 0A7. 96 pages, 9.95 CAD, Paper.

Firefly Encyclopedia of Animals. By Philip Whitfield. 2014. Firefly Books Ltd., 50 Staples Avenue, Unit 1, Richmond Hill, ON, Canada, L4B 0A7. 256 pages, 19.95 CAD, Paper.

Firefly Encyclopedia of Dinosaurs and Prehistoric Animals. By Douglas Palmer. 2014. Firefly Books Ltd., 50 Staples Avenue, Unit 1, Richmond Hill, ON, Canada, L4B 0A7. 256 pages, 19.95 CAD, Paper.

Minutes of the 135th Annual Business Meeting of the Ottawa Field-Naturalists' Club January 14, 2014

Place and time: Fletcher Wildlife Garden, Ottawa, Ontario, 7:00 pm
Chairperson: Fenja Brodo, President

Over 30 attendees spent the first half-hour reviewing the minutes of the previous ABM, the financial report and the OFNC committees' annual reports for 2012-2013. The meeting was called to order at 7:30 pm with some opening remarks from the President.

1. Minutes of the Previous Annual Business Meeting

It was moved by Annie Bélair and seconded by Rémy Poulin that the minutes of the 134th Annual Business Meeting be accepted as distributed.

Carried

2. Business Arising from the Minutes

Nil.

3. Communications Relating to the Annual Business Meeting

Nil.

4. Treasurer's Report by Ken Young

Ken started by explaining that the OFNC uses a "fund accounting" system. This means that the revenues and expenses for some OFNC activities are segregated; each of these is a fund. A side effect is that the financial statements do not include a single table presenting all the revenues and expenses of the Club. Instead there are separate statements for different types of fund. Therefore Ken distributed a separate table showing a statement of operations and changes in fund balances for all OFNC funds.

All the funds except one are "restricted". This means that the revenues of the fund can only be spent on the purpose established for the fund. One fund is "externally restricted". That is the Macoun Camfield Endowment, which results from a legal agreement made between the donor (the Camfield family, in memory of Martha Camfield who passed away in 2010) and the OFNC. This money in this fund is used to earn interest. Half of the interest is reinvested to maintain the value of the fund, and half is used to develop the Macoun Field Club. The other restricted funds are based on restrictions that were established internally, by the OFNC.

There is one unrestricted fund, the "General Fund", which accounts for most revenues and expenses of the Club.

These funds, then, are used to organize the revenues and expenses of the OFNC. In the financial statements, details about the General Fund are on page 3, the internally restricted funds are on page 4 and the externally restricted fund is on page 5. The Statement of Financial Position on page 2 is for the aggregate of all funds; it is equivalent to the Balance Sheet of a for-profit business. The Statement of Cash Flows on page 6 is also for all funds taken together.

Starting in 2014, a new internally restricted fund will be created for the Fletcher Wildlife Garden.

Ken then drew our attention to the financial results. Net revenues for 2013 were positive for a second year, so the Club is in a good position financially.

As for the 2014 budget, it was approved by Council in November 2013; it is attached to the minutes of that meeting and is available on the OFNC website where minutes of Council meetings are kept, at http://ofnc.ca /council/minutes.php.

Fenja thanked Ken for his presentation, and for his hard work as treasurer.

Motion: It was moved by Ken Young and seconded by Rob Alvo that the financial statements be accepted as a fair representation of the financial position of the Club as of September 30, 2013.

Carried

5. Nomination of the Accountant

Moved by Ken Young and seconded by Barbara Chouinard that the accounting firm of Welch LLP be nominated to conduct a review of the OFNC's accounts for the fiscal year ending September 30, 2014.

Carried

6. Committee Reports

The annual committee reports serve as a record of what the OFNC does throughout the year. A copy had been distributed to attendees at the beginning of the meeting.

Moved by Annie Bélair and seconded by Ernie Brodo that the reports be accepted as distributed.

Carried

Some notes:

a. The Birds Committee's annual report states that "members of the committee were active as volun-

teers with the very successful BirdLife International World Congress held in Ottawa in the summer of 2013." Fenja added that in December 2013, Ian Davidson, member of OFNC Council and executive director of Nature Canada, presented Nature Canada's "Affiliate Award" to formally recognize the OFNC's contribution to the phenomenal success of the congress.

b. As of January 2014, the Excursions and Lectures Committee will be called the Events Committee.

c. The Finance Committee's annual report reflected the fact that at the time of writing the report, the OFNC financial statements were not finalized and it was thought that a small deficit may be the result for the period. Now that the financial statements are finalized, the result is a profit. This is the reason for the discrepancy.

d. Dan Brunton pointed out that the Publications Committee's annual report states that the "challenge of getting *The Canadian Field-Naturalist* (CFN) back on schedule has been virtually achieved." He announced that issue 127(4), the last issue of 2013, was electronically sent to subscribers on the day of this meeting, meaning the CFN is indeed back on schedule. The crowd applauded to congratulate the CFN publishing team.

7. OFNC's Twitter Accounts and Blog

Natalie Sopinka, new member of the Education and Publicity Committee, introduced herself and described some of the new social media initiatives that were launched:

The OFNC now has three Twitter accounts: one for the CFN, one for the Fletcher Wildlife Garden and one for the OFNC in general.

A WordPress-based blog has been created (http://ofnc.wordpress.com) for reports of monthly meetings and events, as well as local nature-related information. It is being monitored by members of the Education and Publicity Committee. An email was distributed to OFNC members to announce its launch and an article on the subject will be published in *Trail & Landscape*.

She invited everyone to follow the Twitter accounts and the blog, and said that anyone is welcome to write entries for the blog.

8. Report of the Nominating Committee A. MacKenzie

Relevant Excerpts from the OFNC Constitution (revised February 2000)

Article 8 – "The Council shall consist of the officers of the Club and up to eighteen additional members, all members of the Club."

Article 12 – "The officers of the Club and other members of the Council shall be elected annually at the Annual Business Meeting. The nomination of sufficient persons for election to the various offices and membership of the Council shall be the responsibility of the Nominating Committee, which shall act in the manner prescribed in the By-Laws.

The Council shall, at the earliest possible date, appoint chairs and members of Standing and ad hoc committees and Editor and Business Managers, as required for club publications."

NOMINATED OFFICERS	OFFICIAL DUTY
Fenja Brodo	President
Henry Steger	1st Vice-President
Eleanor Zurbrigg	2nd Vice-President
Annie Bélair	Recording Secretary
Ken Young	Treasurer

NOMINATED OTHER MEMBERS (in alphabetical order)

Daniel Brunton	Don Hackett
Carolyn Callaghan	Diane Kitching
Barbara Chouinard	Ann MacKenzie
Julia Cipriani	Karen McLachlan Hamilton
Owen Clarkin	Lynn Ovenden
Barry Cottam	Rémy Poulin
Ian Davidson	

Motion: Moved by Ann MacKenzie and seconded by Diane Lepage that this slate of nominees be accepted as members of the Council of the OFNC for 2014.

Carried

Fenja thanked David Hobden, Diane Lepage and Jeff Skevington who will not be returning to Council in 2014; she welcomed Julia Cipriani, now chair of the Events Committee, who is rejoining Council.

9. Review of OFNC Constitution and Bylaws for New Regulations

Ann MacKenzie, Chair of the Constitution Committee, gave a presentation on the likely implications to the OFNC of the pending changes to the Ontario *Not-for-Profit Corporations Act*. Changes are anticipated to our classes of membership, to the Council and with respect to the notification and voting related to the Annual Business Meeting. It is expected that a revised constitution will be ready for members approval at the January 2016 Annual Business Meeting. The club is working with lawyers and will notify members when there is a revised version for their consideration and comment.

10. In Remembrance

The OFNC noted with sadness the passing during 2013 of three members who had made a notable contribution to the club and the naturalist community:

Gordon Pringle – died in February 2013. A key member of the Birds Committee and the Birds Records Subcommittee, which he chaired.

Violetta Czasak – died in May 2013. She named the OFNC as sole beneficiary of her estate.

Bob Bracken – died in July 2013. A great naturalist of the Ottawa area who started out as a member of the Macoun Field Club.

11. Adjournment

Moved by Henry Steger and seconded by Rob Alvo that the meeting be adjourned at 8:45 pm.

Carried

ANNIE BÉLAIR
Recording Secretary

The Ottawa Field-Naturalists' Club 2012-2013 Annual Reports

Awards Committee

The Awards Committee manages the process to annually recognize those OFNC members and other qualified persons who, by virtue of their efforts and talents, are deserving of special recognition. In 2013, nominations were received and evaluated (see awards criteria http://www.ofnc.ca/awards.php), seven nominations were recommended to Council for approval, and biographies were written for publication in the Club's journals. The awards were presented at the annual Soiree in April. The recipients' names, type of award(in brackets) and rationale for recognition follow below:

- Dr. J. Bruce Falls (Honorary Member) For his immense contribution to the investigation, documentation and protection of natural features and landscapes in Ontario and throughout Canada.
- Peter Hall (Honorary Member) For his work on butterflies among other species, the Fletcher Wildlife Garden and biodiversity conservation, and for over 30 years of service to the Club.
- Jay Fitzsimmons (Member of the Year) – For his work managing the electronic publishing of *The Canadian Field-Naturalist* (CFN) and also for his enthusiastic and far-reaching promotion of the journal.
- Connie Clark (George McGee Service) – For over 10 years of active service with the Fletcher Wildlife Garden, leading walks for the Club, committee work and writing *Trail & Landscape* articles.
- David Seburn (Conservation Award – Member) For significant efforts for over a decade in turtle research and conservation in the Ottawa area.
- Biodiversity Conservancy International and the National Capital Commission (Conservation Award – Non-Member): PT Dang (President BCI), Eva Katic (NCC) – For the sand dune conservation project at the Pinhey Forest in Ottawa.
- Diane Lepage (Anne Hanes Natural History Award) – For her independent study of and publication in *Trail & Landscape* on the moths of the Larose Forest.

Committee members: Irwin Brodo, Julia Cipriani, Christine Hanrahan, Ann MacKenzie

ELEANOR ZURBRIGG, Chair

Birds Committee

The Birds Committee organized the Fall Bird Count (2012) and along with the Club des Ornithologues de l'Outaouais participated in the 2012 Christmas Bird Count. The Peregrine Falcon Watch 2013 had a mixed season. The pair at the Data Center had a successful year fledging their one chick. However, once again, the downtown pair's eggs did not hatch. The Bird Record Sub-committee met during the year to review rare bird reports and is putting the finishing touches on a new checklist for Ottawa. This project was stalled by the passing of long-time committee member Gordon Pringle who was a key player in the development of the checklist. Members of the committee were active as volunteers with the very successful BirdLife International Congress held in Ottawa in the summer of 2013. Committee members are also involved in bringing the Ontario Field Ornithologist's Annual Conference to Ottawa for 2014. The committee continues to operate a series of bird feeders throughout the Ottawa Greenbelt. The committee is also in discussion with FLAP (Fatal Light Awareness Program) to place a chapter in Ottawa. This program deals with how to avoid the damage caused by bird/window collisions.

CHRIS TRAYNOR, Chair

Conservation Committee

The OFNC conservation committee was officially re-activated in late 2012, following a time of hiatus. In the past year, the CC has tackled a range of conservation issues in Ontario. We have written several letters on conservation matters, such as the issue of cottage lease extensions in Algonquin Park, the issue of overly enthusiastic mowing practices of meadow areas by the municipal authorities, and a plan to expand a hydro dam in the town of Almonte downstream from the sensitive Appleton Wetland ANSI. Other similar projects have been initiated such as the impact of housecat predation on wildlife, the implications of a possible oil spill from rail or pipelines on our local ecosystems, the turtles being stranded on the road in the vicinity of Mud Lake and a bioblitz near a proposed landfill site near Carlsbad Springs.

A major focus of the new chair is flora conservation, and to this end a few "personal" projects have been initiated. These include: public walks with emphasis on the ecology of and the how-to of plant identification, and the current status of uncommon, rare, or declining native plants in Eastern Ontario and Western Quebec. In this vein, an inventory of the flora of the Fletcher Wildlife Garden has been initiated and is expected to be completed late 2013 or early 2014.

Many other talented and dedicated members of the OFNC CC continue to work on their own personal conservation projects. A committee meeting will be held in late 2013 to brainstorm about increasing CC member engagement, and new approaches to preserving the ecosystems and indigenous species of our region.

OWEN CLARKIN, Chair

Education and Publicity Committee

The primary duty of this committee is to make the Club, as well as natural history, known to the community. It is responsible for the club's publicity, providing speakers/walks as requested by outside groups, considering special educational projects, assisting with membership drives and coordinating the sale of club materials.

Committee members have diverse skills. We make things and sell them, we write, we edit, we create displays and fly the club banner at local events, we ask people to give nature talks. We have not excelled at PR but there is hope: a new member of the committee will focus on publicizing OFNC events and accomplishments. During the past year, the committee experienced a change in chair, lost a few valued members and gained some new ones. We met 6 times, about every two months.

2012 was a big year for sales of club materials such as bird and butterfly checklists, lanyards, 10× loupes and books. Five new creations bear the club logo: a banner, a bookmark, an OFNC sign atop the entryway sign to the Fletcher Wildlife Garden, a lanyard and a lens-wipe (the latest toy). For next year we are considering how to standardize the use of OFNC's logo and brand across many club activities.

We brought OFNC displays to the Soiree in April, the Lac Deschenes Bird Fair at Andrew Haydon Park in May and an Environment Fair at Place Vincent Massey in June. New this year was a regional selection process for OFNC's sponsorship

of a youth who attended Ontario Nature's Youth Summit in September.

Many club members share their natural history expertise with other community groups. We especially thank the generous souls who said "yes" to requests made directly to OFNC:

- Dave Moore and Bev McBride led a nature walk to Mud Lake for visitors from Friendship Force in June. Dave also presented a birding talk to the Seniors Program at the Unitarian Church in September.
- Eleanor Thomson gave a nature talk to the women's group at the Lord Lansdowne Residence.
- Joan Harvey visited Uplands Catholic School to advise the students about extending their butterfly garden.
- Jeff Skevington and Carolyn Callaghan were judges for the OFNC special awards at the Ottawa Regional Science Fair.

LYNN OVENDEN, Chair

Excursions and Lectures Committee

Over the course of 2013, the excursions and lectures committee coordinated 40 hikes, 5 workshops, 9 monthly meetings, the annual awards celebration and the annual business meeting. In addition to bringing back many tried and true events and leaders, several new events were promoted.

The hikes and workshops covered a wide breadth of topics, including: general natural history (6), birds (15), insects (8), spiders (1), plants (8), amphibians and reptiles (3), mammals (1), fish (1), nature photography (1), lichens (1) and fungi (1). Highlights included workshops on invasive plants, lichens, nature photography, arthropods of your home and crane flies, as well as a tour of our national insect collection, an overnight trip to the Kazabazua sand-plain, our annual butterfly count and an exploration of Brewer Pond life. Monthly meetings continued to be held in the Museum of Nature and included talks on birds (5), mammals (1), conservation (1), canoeing (1) and salamanders (1). Committee members included Rob Alvo, Holly Bickerton, Julia Cipriani, Hume Douglas, Jakob Mueller and Jeff Skevington (chair). If you have any new ideas for events or would like to be a leader, please contact Jeff (jhskevington@gmail.com) or other members of the committee.

JULIA CIPRIANI, Committee Member

Finance Committee

As a result of the major changes to the OFNC's financial reporting systems over the last couple of years, Council continues to benefit from the now smoothly running financial reporting system. With the revision of the OFNC's detailed chart of accounts last year, information is now more accurate and detailed with respect to the club's revenues and expenditures. The financial reports provided by the OFNC Treasurer several times a year are a useful tool for Council and committees.

The Finance Committee met several times during the 2012/ 2013 fiscal year to discuss several issues. In March, the Finance Committee proposed a new methodology in allocating investment income. This was done to make the allocation of interest income less complicated at year end. This new methodology was approved by Council, the Camfield Family and the OFNC's auditor.

In May, the Finance Committee was asked to update Council on the current status of honoraria in the OFNC. This information was presented to Council, and a motion was made to resume the honorarium paid to the CFN Manager. This motion was passed by Council.

Lastly, in September, the 2014 budget discussions resulted in a motion to provide FWG with their 2013 budgeted funds. However, in the future, no funds will be transferred to FWG without prior approval through the budgetary process. This is to bring FWG in line with all the other OFNC committees. Budgets are determined by each respective committee, and Council approves the budget. Payment is then made upon approved expenses against the budget. This process provides greater transparency and allows for the timely matching of revenues and expenses.

The club is continuing to run a deficit though it is projected to be lower this year than in recent years. With an improved financial reporting system, it is easier to identify the issues. There are areas that the Finance Committee intends to review in the near future for Council's consideration. This would include issues such as the uncollectible subscriptions invoices, the decrease in OFNC membership numbers, the possible restriction of access to the electronic CFN to only paid members and the declining CFN institutions subscription revenue.

BARBARA CHOUINARD, Chair

Fletcher Wildlife Garden

This is been a busy year for the Fletcher Wildlife Garden. All of the usual activities have proceeded apace, along with a number of other activities, events and achievements. Many of these have involved other groups. Several subcommittees have worked on a number of changes to how things get done at the FWG. This report presents highlights of these as they occurred throughout the year.

Our year kicked off on April 7 with a Spring Fling, inspired by the successful end-of-2012 potluck for volunteers. This was more than a social event, as group and habitat managers provided volunteers with work plans and the FWG treasurer gave an overview of the financial situation. On April 9, the first meeting in several years between Agriculture and Agri-Food Canada and FWG representatives proved productive, with a number of issues being addressed. We have had a very positive working relationship with AAFC and continue to maintain this relationship through other means, such as the Central Experimental Farm Advisory Committee (CEFAC).

Shell grant: FWG's application for funding to dredge the pond and do related work, approved by council and AAFC, was not accepted by the Shell FuellingChange program. Further effort is in abeyance pending the results of an environmental assessment by Environment Canada.

FWG Volunteer Groups: The Butterfly Meadow group and the Friday morning group continued to expand in scope through the hard work of volunteers under the able direction of their managers. The Tuesday Invasive Species Group was much reduced in numbers and hours of operation in a take-stock year, trying to assess the value of its efforts in regard to DSV. This highly successful invasive plant is a limiting factor in our efforts to improve and maintain the habitats. Rather than attempting to cover the FWG as a whole, specific areas were targeted for intensive effort. Brush cutters were tested for effectiveness and AAFC mowed a couple of monocultural stands of DSV in July. Inventories and maps of invasive shrubs and trees are being prepared. The October annual meeting of the Ontario Invasive Plant Council provided, as in the past, useful information on both current research and attempts by other organizations to control invasives. The Monarch Way Station was the focus of milkweed planting work bees in June and

September. Planting, DSV removal and development of the Bill Cody Fern Garden continued in the Ash Woods. A job description for Habitat Managers is in final stages of preparation. Outreach to potential volunteers through our membership in Volunteer Ottawa has been more consistent and successful this year.

Activities involving Outside Organizations: A number of organizations participated in special work projects and other events. These included two full days from the Stewardship Rangers, a return visit from PricewaterhouseCoopers, and 80 students from a Carleton University environmental studies class. Walks and tours were undertaken by several outside organizations, including the Canadian Wildlife Federation and the Ottawa Horticultural Society. The FWG was a site for the inaugural Ottawa Sustainability Tour, although we had more volunteers on hand as greeters than tour participants. A potentially useful liaison with a professor in the Carleton University Biology department was established. The OFNC Bug Day, held at the Interpretation Centre/Backyard Garden, was a roaring success.

Research: The FWG has been the object of new research this year. Researchers from the Invasive Species Centre in Sault Ste Marie and the University of Guelph Microbiology Department are conducting several experiments in attempts to understand the soil chemistry of a number of 'mystery' circles, found at various locations. These circles are characterized by a lack of DSV within and a perimeter of small, yellowed DSV plants, with normal DSV growth beyond. Even more significantly, the FWG is slated to be one of the test sites for the release in 2014 of larvae of the moth *Hypena opulenta* that feed on the leaves of DSV. Special notice must be given to completion this year of Renate Sander-Regier's PhD thesis on the FWG, "The Power of a Small Green Place: A case study of Ottawa's Fletcher Wildlife Garden."

Communications: The newsletter has been resurrected and revamped by our new editor; the photo galleries on PBase continue to be well received; the website is recovering from a loss of data; social media including Facebook and twitter provide further outreach.

Interpretation Centre: A job description was drawn up for the new role of Interpretation Centre manager. Two OFNC members volunteered and they started in September.

Finances and first budget: The annual plant sale, our major fundraising effort, was very successful again this year, raising about $4000.00. While questions remain regarding the relationship between OFNC and FWG funds, recent attempts to clarify them have resulted in the first ever annual budget for the FWG.

Management: The management committee continues to operate with a rotating chair. This is working reasonably well in regard to month-to-month business. However, the roles of the chair and the MC and other matters such as longer-term planning and council's role with regard to the FWG are up for discussion. The lease and collaborative agreements between AAFC and the OFNC are to be renewed by April 1, 2014. Preliminary discussions between the parties have been positive. Our year wraps up with a fall potluck on November 24.

BARRY COTTAM, Committee Member

Macoun Field Club Committee

The Committee held one planning meeting ahead of the Macoun Club's start-up in September and put together the month-to-month program by telephone and e-mail. An up-to-date schedule and illustrated record of the weekly activities was maintained on its website (macounfieldclub.ca). Committee members supervised or gave presentations at 19 indoor meetings and led 15 regular field trips during the school year; they also led another four special trips, two jointly with the OFNC and two with SOS Dunes (Pinhey Sand Dunes). Indoor sessions were held in the Fletcher Wildlife Garden's Interpretation Centre. Most field trips took place either at the Macoun Club's nature-study area in Stony Swamp or on private properties in Lanark County. The Committee produced issue no. 67 of the Club's annual publication (*The Little Bear*), and the seventh and eighth annual notebooks of sightings in the Stony Swamp study area (bound in hard cover), all for distribution to members.

ROBERT E. LEE, Chair

Membership Committee

The distribution of the membership for 2013 on September 30, 2013 is shown in the table below, with the corresponding numbers for 2012 shown in brackets. "Others" represent, for the greatest part, affiliate organizations that receive complimentary copies of the Club's publications. The decrease in total membership of 28 continues a long-term overall trend but one that follows an average reduction of 21 per year during the period from 2006 to 2012. Local membership (within 50 km of Parliament Hill) decreased to 617 from 633 in 2013 and 2012, respectively.

HENRY STEGER, Chair

	CANADIAN		USA		OTHER		TOTAL	
	2013	2012	2013	2012	2013	2012	2013	2012
Individual	324	(351)	12	(13)	0	(0)	336	(364)
Family	288	(285)	0	(1)	1	(1)	289	(287)
Student*	11	(10)	0	(0)	0	(0)	11	(10)
T and L	2	(3)	0	(0)	0	(0)	2	(2)
Honorary	21	(21)	0	(0)	0	(0)	21	(21)
Life	45	(47)	1	(3)	1	(1)	49	(51)
Other	23	(23)	1	(0)	1	(1)	24	(24)
TOTAL	714	(740)	15	(17)	3	(3)	732	(760)
	324	(351)	12	(13)	0	(0)	336	(364)

*Student Membership was initiated in Year 2012 and is intended to encourage interest in natural history among high school and university students.

Publications Committee

Publications Committee members in 2013 were Carolyn Callaghan, Paul Catling, Jay Fitzsimmons, Sandra Garland, Tony Gaston, Karen McLachlan Hamilton, William Halliday, Elizabeth Morton, Frank Pope, Jeff Saarela and Dan Brunton (chair). We met formally twice during the year to discuss a wide variety of issues and to provide advice and information to both the OFNC Council and to the editorial teams. A great number of informal communications were also conducted electronically amongst committee members on a variety of publication topics, primarily in regards to *The Canadian Field-Naturalist*.

The challenge of getting *The Canadian Field-Naturalist* back on schedule has been virtually achieved. This is the result of several years of tremendous effort by the current and former editorial teams. Editor-in-Chief Carolyn Callaghan has overseen the publication of five issues of the journal this year, 126(3) through 127(3). The final issue of the 2013 volume is to be posted and circulated within the first few weeks of 2014. With the journal entirely back on schedule, we expect the publication of four issues in 2014.

As many manuscripts had been received by October 2013 as had been received in all of 2012, which already had seen a 20% increase over recent years. We take this as confirmation of the journal's increasingly appeal for the appropriate and timely documentation of important field-oriented natural sciences research. Great strides have also been made by Journal Manager Jay Fitzsimmons and others in the unglamorous but critical area of publication production, with efficiencies achieved with indexing and improved printing turn-around times. Colour images continue to enhance the appearance of more papers than was possible in years past.

All in all, progress has been most encouraging. The full achievement of a 'normal' publication schedule for *The Canadian Field-Naturalist* will now allow us to put more focus on logistical and administrative improvements. That will simplify production and make life easier both for the members and subscribers receiving the journal and for the largely volunteer effort required to make these happen.

Editor Karen McLachlan Hamilton and her team produced the four issues of *Trail & Landscape* in their usual timely and efficiently manner. *Trail & Landscape* fulfills an important newsletter function and also continues to document important ecological information on the regional biodiversity and its conservation needs.

Discussions of a possible special publication addressing the biodiversity of an important Ottawa Valley natural area were initiated in 2013. This may proceed to the production of a stand-alone document in 2014.

DANIEL F. BRUNTON, Chair

Treasurer's Report

Financial Position: At the time of writing, the Financial Statements have not been finalized. However, it appears that revenues will exceed expenses.

Insurance: This year, our insurance coverage was expanded to include Directors' & Officers coverage as well as Commercial General Liability.

Committee Budgets: This year more attention was paid to the preparation of the annual budget. As a result the budget presents a more comprehensive forecast of OFNC revenues and expenses than in the past.

Violetta Csazak Bequest: The Club received a bequest from Violetta Czasak. I have been appointed as executor of the estate. We are proceeding with the sale of her condominium, but in the current real estate market this is a slow process.

Routine Events: Most of the Treasurer's duties continue from one year to the next. They include:

- Filing the Charities Information Report with the Canada Revenue Agency;
- Preparing T4A returns for people receiving honoraria or contract fees from the Club;
- Obtaining Proof of Insurance certificates for Club events;
- Updating the Club's information with our bank, the Canadian Imperial Bank of Commerce, and our online payments processor, PayPal;
- Depositing cheques received and writing cheques to pay expenses;
- Making financial reports to Council and Committees, such as for *The Canadian Field-Naturalist*, the Seedathon, the Fletcher Wildlife Garden and the Macoun Field Club.

I would like to express my appreciation for all the assistance that I have received from Frank Pope, the past Treasurer, and Ann MacKenzie, who handles the investment activities of the Club.

KEN YOUNG, Treasurer

Review Engagement Report

To The Members of THE OTTAWA FIELD-NATURALISTS' CLUB

We have reviewed the statement of financial position of The Ottawa Field-Naturalists' Club as at September 30, 2013 and the statements of operations, changes in fund balances and cash flows for the year then ended. Our review was made in accordance with Canadian generally accepted standards for review engagements and accordingly consisted primarily of enquiry, analytical procedures and discussion related to information supplied to us by the club.

A review does not constitute an audit and consequently we do not express an audit opinion on these financial statements.

Based on our review, nothing has come to our attention that causes us to believe that these financial statements are not, in all material respects, in accordance with Canadian accounting standards for not-for-profit organizations.

CHARTERED ACCOUNTANTS
Licensed Public Accountants

Welch LLP

Ottawa, Ontario
December 23, 2013

The Ottawa Field-Naturalists' Club
Statement of Financial Position
September 30, 2013

	2013	2012
ASSETS		
CURRENT ASSETS		
Cash and cash equivalents (note 4)	$55,862	$156,201
Short-term investments (note 4)	–	43,817
Amounts receivable	24,380	16,138
Prepaid expenses	633	1,403
	80,875	217,559
LONG-TERM INVESTMENTS (note 4)	537,456	386,170
	$618,331	$603,729
LIABILITIES AND FUND BALANCES		
CURRENT LIABILITIES		
Accounts payable and accrued liabilities	$3,582	$2,283
Deferred revenue	16,683	21,239
	20,265	23,522
LIFE MEMBERSHIPS (note 5)	–	1,240
FUND BALANCES		
General fund	317,208	303,378
Internally restricted funds	244,376	239,689
Martha Camfield endowment fund	36,482	35,900
	598,066	578,967
	$618,331	$603,729

Approved by Council:

.... President

.... Treasurer

(See accompanying notes)

PREPARED WITHOUT AUDIT

The Ottawa Field-Naturalists' Club
Statement of Operations and Changes in Fund Balance – General Fund
Year Ended September 30, 2013

	2013	2012
REVENUES		
Membership fees	$ 28,703	$ 30,308
Donations and bequests	27,149	21,954
The Canadian Field-Naturalist		
– subscription revenue	26,153	32,463
author charges	28,234	27,984
Fletcher Wildlife Garden	4,395	5,684
Pelee Trip	–	14,375
Interest income	13,744	12,465
Advertising	1,675	
Other	1,828	680
	131,881	145,913
EXPENSES		
OPERATING:		
Affiliation fees	450	225
Bookkeeping	4,941	6,525
Courier and postage	359	319
Insurance	1,245	782
Interest and bank charges	1,400	1,471
Membership	1,000	1,347
Professional fees	2,800	2,000
Website	3,500	710
General and miscellaneous	3,452	2,697
	19,147	16,076
ACTIVITY:		
The Canadian Field-Naturalist	78,600	52,758
Fletcher Wildlife Garden	7,604	19,012
Awards committee	534	372
Soiree – net	87	(184)
Birds Committee	1,010	971
Donations	–	5,000
Education and publicity	1,829	381
Excursions and lectures	1,953	1,445
Macoun Club	301	555
Pelee Trip	–	11,049
Trail and Landscape	6,986	7,558
	98,904	98,917
TOTAL EXPENSES	118,051	114,993
NET REVENUES	13,830	30,920
FUND BALANCE, BEGINNING OF YEAR	303,378	272,458
FUND BALANCE, END OF YEAR	$317,208	$303,378

The Ottawa Field-Naturalists' Club
Statement of Changes in Fund Balance – Martha Camfield Endowment Fund
Year Ended September 30, 2013

	2013	2012
Fund Balance, Beginning of Year	$ 35,900	$ 35,268
Interest	582	632
Fund Balance, End of Year	$ 36,482	$ 35,900

Note: The interest above represents half of the interest generated by the fund, which is reinvested in the capital of the fund. The other half of the interest is recognized as interest revenue of the Macoun Fund and is made available for the use of the Macoun Field Club.

The Ottawa Field-Naturalists' Club
Statement of Cash Flows
Year Ended September 30, 2013

	2013	2012
Cash Flows from Operating Activities		
Net revenues – all funds	$ 18,517	$ 33,275
Adjustments for:		
Amounts receivable	(8,242)	17,345
Investments	(16,031)	(15,956)
Prepaid expenses	770	(1,113)
Accounts payable and accrued liabilities	1,299	(11,329)
Deferred revenues	(4,556)	7,518
Life memberships	(1,240)	(2,120)
	(9,483)	27,620
Cash Flows from Financing Activities		
Purchase of investments	(137,178)	(120,000)
Proceeds from maturity of investments	45,740	46,043
	(91,438)	(73,957)
Cash Flows from Financing Activities		
Endowment interest reinvested	582	632
Increase (Decrease) in Cash and Cash Equivalents	(100,339)	(45,705)
Cash and Cash Equivalents at Beginning of Year	156,201	201,906
Cash and Cash Equivalents at End of Year	$ 55,862	$ 156,201

Note: Cash equivalents include fixed income investments maturing within three months

(See accompanying notes)

PREPARED WITHOUT AUDIT

The Ottawa Field-Naturalists' Club
Statement of Operations and Changes in Fund Balances – Internally Restricted Funds
Year Ended September 30, 2013

	General Reserve for Contingencies	Manning Fund	Seedathon Fund	Anne Hanes Memorial Fund	De Kiriline Lawrence Fund	Macoun Fund	2013 Total	2012 Total
Revenues								
Donations	$	$ 100	$ 1,130	$	$	$ 1,425	$ 2,655	$ 3,500
Interest		3,888		-		582	4,470	6,163
	-	3,988	1,130			2,007	7,125	9,663
Expenses								
CFN author support	-			-				6,051
Donations			-					313
Seed			1,110				1,110	944
Macoun activities		–				1,253	1,253	
Other				75		-	75	
	-		1,110	75	-	1,253	2,438	7,308
Net Revenues (Expenses)		3,988	20	(75)		754	4,687	2,355
Fund Balances, Beginning of Year	100,000	119,803	788	596	13,384	5,118	239,689	237,334
Fund Balances, End of Year	$100,000	$123,791*	$ 808	$ 521	$ 13,384	$ 5,872	$244,376	$239,689

* includes principal of $100,000 plus undistributed income of $23,791.

(See accompanying notes)

PREPARED WITHOUT AUDIT

The Ottawa Field-Naturalists' Club
Notes to the Financial Statements
Year Ended September 30, 2013

1. Purpose of Organization and Tax Status

The Ottawa Field-Naturalists' Club (the "club") is a registered charitable organization incorporated under the Corporations Act of the Province of Ontario. The club promotes the appreciation, preservation, and conservation of Canada's natural heritage, encourages the investigation, publishes the results of research in all fields of natural history, and diffuses the information to the public and supports and cooperates with other organizations engaged in preserving, maintaining and restoring environments of high quality for living things.

The club is a registered charity, and is exempt from income taxes by virtue of section 149(1)(f) of the Income Tax Act (Canada).

2. Significant Accounting Policies

Basis of accounting

These financial statements have been prepared in accordance with Canadian accounting standards for not-for-profit organizations.

Revenue recognition

(i) The club follows the deferral method of accounting for contributions. Restricted contributions are recognized as revenue in the year in which the related expenses are incurred. Unrestricted contributions are recognized as revenue when received or receivable if the amount to be received can be reasonably estimated and collection is reasonably assured. Endowment contributions are recognized as direct increases in net assets.

(ii) Membership fees are recognized as revenue proportionately over the fiscal year to which they relate. The club's membership year is January 1 to December 31. The portion of membership fees that are received but not yet recognized as revenue are recorded as deferred revenue.

(iii) Subscription revenue is recognized as revenue at the time of shipment of the related publication. The liability for the portion of subscription revenues invoiced in advance of shipment is recorded as deferred revenue.

(iv) Advertising revenue is recognized in the period in which the advertisement is published.

(v) Interest income comprises interest from cash and cash equivalents and investments. Interest on cash equivalents and investments is recognized over their term using the effective interest method. Interest income derived from the investment of restricted contributions, where the contribution agreement specifies that the investment income is restricted, is accounted for the same manner as the restricted contributions.

Fund accounting

The Club maintains its accounts in accordance with the principles of fund accounting. Resources are classified for accounting and reporting purposes into funds according to the activity or object specified.

(i) General Fund

The General Fund reports revenue and expenses relating to general operations and administration activities.

(ii) Martha Camfield Endowment Fund

The Martha Camfield Endowment Fund was established by the family and friends of Martha Camfield to help continue her efforts to have children study, understand, respect and preserve their natural environment. Half of the interest generated by the fund is reinvested in the capital of the fund while the other half of the interest generated is made available only for the use by the Macoun Field Club (the Macoun Fund).

(iii) General Reserve

The General Reserve For Contingencies was established by the Club to fund outstanding operating expenses should the Club discontinue its operations.

(iv) Manning Fund

The Manning fund was established by a bequest, and the interest generated is used to assist authors to publish articles in The Canadian Field-Naturalist.

(v) Seedathon Fund

The Seedathon fund collects donations from the annual bird sighting event and purchases seed for the Club's bird feeders.

(vi) Anne Hanes Memorial Fund

The Anne Hanes Memorial fund was raised in memory of Anne Hanes, the founding editor of Trail and Landscape, and is used to finance the annual winners of the Anne Hanes Natural History Award.

(vii) De Kiriline-Lawrence Fund

The de Kiriline-Lawrence fund was funded by a bequest from the popular author of nature books, and is supplemented by annual donations and used to support conservation efforts.

(viii) Macoun Baillie Birdathon Fund

The Macoun Baillie Birdathon fund recognizes the donations and pledges based upon the number of bird sightings in the one day birdathon sponsored by Bird Studies Canada, and is used to support the Macoun Field Club, a youth club.

Financial Instruments

The Club initially measures its financial assets and financial liabilities at fair value adjusted by transaction costs in the case where a financial asset or financial liability is subsequently measured at cost or amortized cost. The club measures all

of its financial assets and financial liabilities at cost or amortized cost.

Cash and cash equivalents

Cash and cash equivalents include highly liquid investments with maturities of three months or less.

Capital assets

Capital assets are expensed in the year of acquisition.

Donated services

The club is dependent on the voluntary service of many of its members. As there is difficulty in determining the fair value of voluntary services, they are not recognized in these financial statements.

Internally restricted net assets

Internally restricted net assets represent the amount approved by the Council to be set aside for special purposes. These amounts are not available for unrestricted purposes without the approval of Council.

Use of estimates

The preparation of financial statements in conformity with Canadian accounting standards for not-for-profit organizations requires management to make estimates and assumptions that affect the reported amounts of assets and liabilities and disclosures of contingent assets and liabilities at the date of the financial statements and the reported amounts of revenues and expenses during the reporting period. Actual results could differ from these estimates.

Estimates and underlying assumptions are reviewed on an ongoing basis. Revisions to accounting estimates are recognized in the year in which the estimates are revised and in any future years affected.

3. Financial Instruments

The club is exposed to various risks through its financial instruments. The following analysis provides a measure of the club's risk exposure and concentrations as at September 30, 2013.

Credit risk

The club is exposed to credit risk resulting from the possibility that parties may default on their financial obligations, or if there is a concentration of transactions carried out with the same party, or if there is a concentration of financial obligations which have similar economic characteristics, that could be similarly affected by changes in economic conditions, such that the club could incur a financial loss. The club does not hold directly any collateral as security for financial obligations of counterparties.

The club's maximum exposure to credit risk represents the carrying value of its cash, amounts receivable and investments, totalling $617,698 (2012 - $602,326).

The club's cash is deposited with Canadian financial institutions; as a result management believes the risk of loss on cash to be remote. The cash equivalents and investments consist primarily of government bonds and guaranteed investment certificates of Canadian financial institutions of high credit quality. Possible changes to the credit quality of these securities exposes the club to credit risk. The club manages its exposure to this risk by holding a diversified portfolio with varied maturities. The club reduces its exposure to credit risk on its amounts receivable by reviewing the accounts on a regular basis, following up on outstanding amounts and creating an allowance for doubtful accounts when applicable.

An allowance of $1,160 for impairment has been recorded against the amounts receivable.

Liquidity risk

Liquidity risk is the risk that the club cannot meet its debts when they become due. Liquidity risk also includes the risk of the club not being able to liquidate assets in a timely manner at a reasonable price.

The club meets its liquidity requirements by monitoring its expected future cash flow requirements and holding a significant amount of assets that can be readily converted into cash.

Market risk

Market risk is the risk that fair value or future cash flows of a financial instrument will fluctuate because of changes in market prices. Market risk is comprised of currency risk, interest rate risk and other price risk.

Currency risk

Currency risk refers to the risk that the fair value of financial instruments or future cash flows associated with the instruments will fluctuate relative to the Canadian dollar due to changes in foreign exchange rates.

Approximately $18,000 (2012 - $14,000) of club's cash and cash equivalents are denominated in U.S. currency. However, the club primarily transacts in Canadian dollars. As a result, management does not believe it is exposed to significant currency risk.

Interest rate risk

Interest rate risk refers to the risk that the fair value of financial instruments or future cash flows associated with those instruments will fluctuate due to changes in market interest rates. The exposure of the club to interest rate risk arises from its interest bearing assets.

The club's cash includes amounts on deposit with Canadian financial institutions that earn interest at market rates. Fluctuations in market rates of interest on cash do not have a significant impact on the club's financial operations.

The club manages the interest rate risk of its cash equivalents and investments by the implementation of prudent investment policies. The club's investments in bonds mature at face value on a staggered basis over the next twelve years. The laddered structure of maturities helps to enhance the average portfolio yield while reducing the sensitivity of the portfolio to the impact of interest rate fluctuations. Effective interest rates to maturity for these securities range from 2.40% to 4.36% (2012 2.58% to 4.75%).

Other price risk

Other price risk refers to the risk that the fair value of financial instruments or future cash flows associated with the instruments will fluctuate because of changes in market prices (other than those arising from currency risk or interest rate risk), whether those changes are caused by factors specific to the individual instrument or its issuer or factors affecting all similar instruments traded in the market.

The club is not exposed to other price risk.

Changes in risk

There have been no changes in the club's risk exposures from the prior year.

4. Cash And Cash Equivalents And Investments

Cash and cash equivalents are comprised of:

	2013 Market Value	2013 Amortized Cost	2012 Amortized Cost
Cash in accounts at fair value	$ 55,862	$ 55,862	$ 88,793
Canadian Western Bank 4.41% due October 9, 2012		–	30,872
CIBC GIC 1.4% due October 12, 2012		–	21,284
Ontario – 4.64% due December 2, 2012		–	15,252
	$ 55,862	$ 55,862	$ 156,201

Short-term investments are comprised of:

	2013 Market Value	2013 Amortized Cost	2012 Amortized Cost
Manitoba – 4.75% due September 5, 2013	–	–	$ 43,817

Long-term investments are comprised of:

	2013 Market Value	2013 Amortized Cost	2012 Amortized Cost
CIBC – 4.19% due October 31, 2014	$ 69,510	$ 67,782	$ 65,056
New Brunswick – 4.30% due December 3, 2015	63,539	60,582	60,850
Home Trust GIC – 2.40% due October 12, 2016	34,175	34,175	–
Ontario Hydro – 4.01% due November 26, 2016	26,600	26,058	25,054
Ontario – 4.07% due December 2, 2017	52,200	48,588	46,687
Ontario – 2.58% due December 2, 2018	62,810	62,861	61,280
British Columbia – 3.74% due March 5, 2019	29,079	27,481	26,491
Newfoundland – 4.36% due January 7, 2020	43,709	40,605	38,908
British Columbia – 3.26% due August 23, 2021	63,438	63,860	61,844
Nova Scotia Power – 2.80% due February 26, 2022	15,904	17,126	–
Hydro Quebec – 3.12% due February 15, 2023	38,423	41,185	–
Manitoba – 3.82% due September 5, 2025	45,936	47,153	–
	$ 545,323	$537,456	$ 386,170

5. Commitments

Life memberships

The club is committed to provide for regular membership benefits to lifetime members. Since it is not practicable to determine the total liability associated with providing these benefits for the rest of the lives of these individuals, the annual costs are expensed as incurred. Lifetime memberships are no longer being offered by the club. As of September 30, 2013, there were 49 (2012 - 51) active lifetime members.

Fletcher Wildlife Garden

The Fletcher Wildlife Garden (FWG) is 6.5 hectare property of the Central Experimental Farm in Ottawa, Ontario and is a long-term project of the club. The FWG is managed by a club committee and maintained by club volunteers. The costs associated with maintaining the property are approximately 2,000 hours of voluntary human resources per year, plus regular maintenance and cleaning supplies. The fair value of the contributed human resources are not recognized in these financial statements.

6. Comparative Figures

Certain comparative figures have been reclassified where necessary to conform to the presentation adopted in the current year.

PREPARED WITHOUT AUDIT

Book Reviews

Mailing date of the previous issue 128(2): 8 July 2014

THE CANADIAN FIELD-NATURALIST Volume 128, Number 3 2014

Articles

Notes

Tributes

(continued on inside back cover)

ISSN 0008-3550

The CANADIAN FIELD-NATURALIST

Published by THE OTTAWA FIELD-NATURALISTS' CLUB, Ottawa, Canada

Volume 128, Number 4 October–December 2014

The Ottawa Field-Naturalists' Club

FOUNDED IN 1879

Patron

His Excellency the Right Honourable David Johnston, C.C., C.M.M., C.O.M., C.M.
Governor General of Canada

The objectives of this Club shall be to promote the appreciation, preservation and conservation of Canada's natural heritage: to encourage investigation and publish the results of research in all fields of natural history and to diffuse information on these fields as widely as possible; to support and cooperate with organizations engaged in preserving, maintaining or restoring environments of high quality for living things.

To communicate with the Club, address postal correspondence to: The Ottawa Field-Naturalists' Club, P.O. Box 35069, Westgate P.O., Ottawa, ON, K1Z 1A2, or e-mail: ofnc@ofnc.ca. For information on Club activities, go to www.ofnc.ca

The Canadian Field-Naturalist

The *Canadian Field-Naturalist* is published quarterly by The Ottawa Field-Naturalists' Club. Opinions and ideas expressed in this journal do not necessarily reflect those of The Ottawa Field-Naturalists' Club or any other agency.

Website: www.canadianfieldnaturalist.ca/index.php/cfn

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COVER: A female *Misumena vatia* on a yellow lady's slipper *Cypripedium parviflorum* in the Burnt Cape Ecological Reserve, Newfoundland. Photo by R. Perry. See pages 363–376 in this issue.

The Canadian Field-Naturalist

Volume 128, Number 4 October–December 2014

The Enigma of the 10-year Wildlife Population Cycle Solved? Evidence that the Periodicity and Regularity of the Cycle Are Driven by a Lunar Zeitgeber

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Archibald, Herbert L. 2014. The enigma of the 10-year wildlife population cycle solved? Evidence that the periodicity and regularity of the cycle are driven by a lunar zeitgeber. Canadian Field-Naturalist 128(4): 327–340.

Despite nearly 100 years of research, the periodicity and regularity of the 10-year wildlife population cycle remain an enigma. This paper presents the hypothesis that the 9.3-year nodal half-cycle of the moon is the zeitgeber ("time-giver") of the 10-year wildlife population cycle. The period of the population cycles of the Snowshoe Hare (*Lepus americanus*) and Ruffed Grouse (*Bonasa umbellus*) is close to 9.3 years. These wildlife cycles have stayed closely in phase with the 9.3-year nodal half-cycle for 150 years. Population density of the Snowshoe Hare and Ruffed Grouse is inversely related to a 9.3-year cycle of the moon's tidal force. There is also a 9.3-year cycle of "nights without darkness" at the equinoxes, in which the full moon rises before sunset and sets after sunrise the following morning in certain years. Snowshoe Hare and Ruffed Grouse cycles are positively correlated with this phenomenon. The nodal cycle provides explanations for the key features of the 10-year wildlife cycle: regularity, periodicity, amplitude, distribution, and synchrony. Population models based solely on the nodal cycle account for 62% of the variation in the Canada Lynx (*Lynx canadensis*) cycle and 37% in the Ruffed Grouse cycle. The mechanism(s) by which herbivore cycles might be entrained by the lunar nodal cycle could involve a cyclic effect on factors including predation, stress, photoperiod, phenology, temperature, cloudiness, ultraviolet B radiation, cosmic rays, and food plant quality.

Key Words: 10-year wildlife cycle; lunar nodal cycle; Snowshoe Hare; *Lepus americanus*; Ruffed Grouse; *Bonasa umbellus*; Canada Lynx; *Lynx canadensis*

Introduction

The 10-year wildlife cycle has been described as an "extraordinary precise metronome" by ecological, if not celestial, standards (King and Schaffer 2001). Yet, despite nearly 100 years of research, the periodicity and regularity of the 10-year wildlife cycle remain an enigma. "The key question of how the 10-year cyclic pattern is produced is still unsolved" (Yan *et al.* 2013).

Numerous hypotheses, involving both endogenous (e.g., disease, predation, food abundance) and exogenous (e.g., weather, sunspots, ultraviolet radiation) causes, have been proposed to explain the cycle (see summaries in Murray [2003] and Zimmerman *et al.* [2008]). Cyclic declines in Ruffed Grouse (*Bonasa umbellus*) have been attributed to increased predation because of a predator shift following decreases in Snowshoe Hare (*Lepus americanus*) numbers (Keith 1963), but this hypothesis has been challenged because Ruffed Grouse tend to peak and decline before Snowshoe Hare (Hoffmann 1958). The prevailing endogenous hypothesis is that the Snowshoe Hare cycle results from the tri-trophic interaction between predation and food supplies, with predation as the dominant factor (Krebs *et al.* 2001). In his review, Rusch (1989) concluded that predation, primarily avian, is responsible for virtually all grouse mortality and the cyclic trend in grouse populations. In their classic paper, Elton and Nicholson (1942) concluded that the broad synchronization of the Canada Lynx (*Lynx canadensis*) cycle "makes it certain that some overriding process maintains the cycle in line over the whole extent of Canada." In his plant stress hypothesis, Selas (2006) posited that the Snowshoe Hare cycle is forced by the sunspot cycle, through its effects on plant productivity caused by changes in ultraviolet B (UVB) radiation. Sinclair *et al.* (1993) hypothesized that Snowshoe Hare cycles are synchronized by the sunspot cycle via its effect on climatic factors. However, a causal relationship between sunspots and the Canada Lynx cycle has been rejected on a statistical basis (Moran 1949; Lindstrom *et al.* 1996). Nilssen *et al.* (2007) demonstrated that the 11-year sunspot cycle cannot explain the 10-year cycle of the Autumnal Moth (*Epirrita autumnata*) in Fennoscandia because the two cycles ran in-phase and then completely out of phase during a 114-year period.

Murray (2003) suggested the possibility that an exogenous factor could entrain or synchronize a cycle that is driven by endogenous forces. Yan *et al.* (2013) concluded that the 10-year hare–lynx cycle is the result of the joint forces of both endogenous and exogenous factors. The ideal exogenous cycle candidate would have a consistent period that matched the wildlife cycle and would shed light on its other unexplained features.

Snowshoe Hare and Canada Lynx populations tend to cycle synchronously across the boreal forests of Canada and Alaska (Krebs *et al.* 2001). Recent explanations of the spatial synchrony of 10-year-cycle species across large geographic regions have generally focused on common weather or climatic perturbations (i.e., Moran effect), dispersal, migration of natural enemies

(Liebhold *et al.* 2004), or a combination thereof. Krebs *et al.* (2013) concluded that the mobile predator hypothesis offers the most likely explanation of the synchrony and traveling waves of hare populations across northwestern North America. Analysis of the spatial synchrony of Canada Lynx populations revealed three large climatic regions in which the phase synchrony is similar, with the continental region 1–2 years ahead of the Pacific and Atlantic (Stenseth *et al.* 1999, 2004). These authors concluded that external climatic forcing associated with the North Atlantic Oscillation acts as a synchronizer within each region, but they offer no explanation for the inter-regional timing of the cycle. Krebs *et al.* (2013) rejected the "attractive" hypothesis that regional weather synchronizes local Snowshoe Hare populations because of the lack of a mechanism whereby weather could drive hare numbers.

The path of the moon across the sky is complicated by its nodal cycle. The 18.6-year lunar nodal cycle gives rise to year-to-year differences in both tidal force and the moon's "altitude" (angle or height in the sky above the horizon). The tidal force of the moon is the difference between the moon's gravitational force on the side of the earth closest to the moon and that on the side farthest from the moon (Kutner 2003). The moon and the sun produce maximum tidal forces at the equinoxes when lunar "declination" (angle relative to the equator) is zero, which happens twice during the nodal cycle or every 9.3 years, and when the sun is directly above the equator, so that solar declination is zero (Pugh 1966). Because the moon's orbit is inclined 5.1° to the earth's orbit (also known as the "ecliptic"), the declination of the moon's orbit ranges from a minimum of 18.3°N and S every lunar month to a maximum of 28.6°N and S every month during the 18.6-year period of the nodal cycle. What the observer at 55°N latitude would see is variation in the moon's altitude from as little as a high of 53.5° and a low of 16.5° two weeks later (monthly swing of 37°) to, 9.3 years later, as much as a high of 63.5° and a low of 6.5° (monthly swing of 57°).

Although the nodal cycle has been known at least as far back as Stonehenge, the biological significance of the 9.3-year nodal half-cycle remains virtually unknown. Archibald (1977) hypothesized that the length and regularity of the period, approximate regional and inter-specific synchrony, and northern geographic distribution of the 10-year wildlife population cycle arise from the 9.3-year half period of the moon's 18.6-year nodal cycle. This hypothesis has been largely ignored or dismissed as a nonsense correlation (Royama 1992), perhaps because Archibald did not provide any evidence of biological effects of the 9.3-year lunar cycle or plausible mechanism. Selas (2014) proposed a new variation of the plant stress hypothesis involving modulation of cosmic rays by a 9.3-year cyclic "lunar index" (i.e., maximum declination cycle) and the 11.1-year sunspot cycle. According to Selas, a low lunar index (i.e., maximum tidal force) increases geomagnetic activity, which reduces incoming cosmic ray particles, which increase protein mobilization and reduce production of secondary metabolites in plants, thereby increasing herbivore forage quality and, hence, enhancing herbivore performance.

The objective of this paper is to present evidence supporting the hypothesis that the 9.3-year half period of the lunar nodal cycle is the zeitgeber (literally "time-giver") of the 10-year wildlife cycle and to speculate on mechanisms by which herbivore cycles might be entrained by the lunar nodal cycle.

Methods

I compiled reports of peaks in Snowshoe Hare and Ruffed Grouse abundance (Table 1) from nine sets of data (Table 2) of several types: density surrogates, such as annual fur returns (MacLulich 1957) or spring drumming counts (Williams *et al.* 2004; Minnesota DNR 2011); simple lists of peak years in an area (Shorger 1947); and lists of peak abundance for multiple locations (Keith 1963; Hodges 2000a,b). In decades where there were two or three consecutive years of similarly high population reported in a dataset or occurring in a species, the median was used as the value of the peak year. None of these datasets is precisely accurate; all have flaws and biases of various kinds. Also, peak years are not directly comparable across species because data are based on different types of records and are from different regions. Nevertheless, the mean peak years computed by averaging across species provide a broad-scale, general picture of the timing of cycle peaks over large geographic areas during the 150-year period covered.

Predicted peak years of abundance in Table 1 were computed using the formula $P_n = 1950.22 \pm 9.3n$, where P_n is the nth peak year after or before 1950.22 (date of the vernal equinox of 1950 when lunar declination reached a peak value, which happens only once in each 18.6-year nodal cycle) and 9.3 is the period of the population cycle (Archibald 1977).

Sun and moon rise and set times were obtained from the Astronomical Sky Calendar (www.briancasey.org/artifacts/astro/skycalendar.cgi) and from the United States Naval Observatory's Complete Sun and Moon for One Day website (http://aa.usno.navy.mil/data/docs/RS_OneDay.php). The number of minutes the full moon was above the horizon at both dusk (moonrise before sunset) and the following dawn (moonset after sunrise) were computed for April and September. Lunar declination data were obtained from the Jet Propulsion Laboratory Horizons Web-Interface (http://ssd.jpl.nasa.gov/horizons.cgi#top). Over the course of the lunar nodal cycle, the moon's declination varies about 5.1° above and below the ecliptic. For each year, the absolute value of the maximum declination from the ecliptic in the equinox month of September was determined at 50°N, 90°W, i.e., absolute value (reported declina-

TABLE 1. Reported and predicted peaks in abundance of the Showshoe Hare (*Lepus americanus*) and the Ruffed Grouse (*Bonasa umbellus*) in northern North America.

Reported peak years of abundance				
Snowshoe Hare	Ruffed Grouse	Mean peak year	Predicted peak years	Difference* (years)
2006.0	2009.0	2007.5	2006.0	1.5
1998.0	1998.5	1998.2	1996.7	1.5
1989.2	1989.0	1989.1	1987.4	1.7
1980.0	1979.2	1979.6	1978.1	1.5
1970.8	1971.8	1971.3	1968.8	2.5
1959.8	1959.5	1959.6	1959.5	0.1
1951.5	1949.2	1950.4	1950.2	0.2
1941.6	1941.2	1941.4	1940.9	0.5
1932.2	1932.6	1932.4	1931.6	0.8
1923.6	1922.6	1923.1	1922.3	0.8
1912.4	1914.2	1913.3	1913.0	0.3
1904.1	1904.6	1904.4	1903.7	0.7
1896.0	1898.0	1897.0	1894.4	2.6
1886.5	1887.0	1886.8	1885.1	1.7
1876.0	1877.0	1876.5	1875.8	0.7
1865.0	1866.0	1865.5	1866.5	−1.0
1857.0	1857.0	1857.0	1857.2	−0.2
Mean (SD)				0.9 (0.91)
Mean period	9.3	9.5	9.4	

Note: SD = standard deviation.
*Between reported and predicted peak years.

TABLE 2. Sources of the reports of peak abundance listed in Table 1.

Species	Date range	Reference	Location	Source type
Snowshoe Hare	1857–1899	MacLulich (1957: 296)	Hudson's Bay Watershed	Fur returns
	1900–1955	Keith (1963: 42)	Northern North America	Peak abundance (median years)
	1956–1992	Hodges (2000a: 119–120	Canada, Alaska	Peak abundance (median years)
	1956–1992	Hodges (2000b: 166–168)	Minnesota, Wisconsin, Manitoba	Peak abundance (median years)
	1993–2011	Krebs (2011: 6)	Yukon Territory	Density on study area
Ruffed Grouse	1857–1899	Schorger (1947: 54)	Wisconsin	Peak years of abundance
	1900–1951	Keith (1963: 57)	Northern North America	Peak abundance (median years)
	1949–2010	Minnesota DNR (2011: 45)	Minnesota	Drumming counts
	1956–2001	Williams *et al.* (2004: 1138)	Northern Wisconsin, North Dakota	Drumming counts

tion -23.5°). September maximum lunar declination and April and September total minutes full moon above horizon were compared for two population datasets: Ruffed Grouse spring drumming counts conducted in Minnesota from 1949 to 2010 (Minnesota DNR 2011) and spring Snowshoe Hare density in the Kluane region of Yukon Territory (Krebs 2011).

Population modeling and preparation of figures were done using SciDaVis (http://scidavis.sourceforge.net/) software. Modeling results were compared with 1949–2010 Minnesota drumming counts and 1842–1918 Canada Lynx fur returns from the Northern Department (Elton and Nicholson 1942). The classic lynx time series is arguably the best example of a near-perfect population cycle with a minimal amount of noise. This dataset was not used, however, for the peak years of abundance analysis (Table 1) because populations of Canada Lynx are not independent of populations of their main prey, the Snowshoe Hare.

Correlation between population size and lunar declination was measured with least squares regression using software supplied by Wessa (Free Statistics Software, Office for Research Development and Education, version 1.1.23-r7, www.wessa.net), even though the assumption of independence of observations in each time series is clearly violated (Liebhold *et al.* 2004).

The inadequacy of currently available correlational measures was pointed out by Liebhold *et al.* (2004): "for cyclic populations, subtle differences in the timing of cycles... may result in low statistical correlation even when populations are closely linked."

Results

The period of the cycles of the Snowshoe Hare and Ruffed Grouse shown in Table 1 is close to 9.3 years: 9.3 and 9.5 years, respectively. Selas (2014) demonstrated that the periods of both the Canada Lynx and the Autumnal Moth cycles are very close to the 9.3-year lunar nodal half-cycle. One point that seems to have been overlooked in the literature, however, is how critical the period length is. For example, if you spin backward from 2006.0 (when lunar declination reached a peak value seen only once in each 18.6-year nodal cycle) using the 9.6-year period suggested by Elton and Nicholson (1942) and Krebs *et al.* (2001), the predicted peak year 15 cycles back is 1862.0, which is almost completely out of phase with the lunar peaks in 1857.2 and 1866.5. In contrast, after 15 cycles back using the 9.3-year period, reported and predicted peaks remain in phase, with the mean herbivore peak of 1857.0 coinciding with the lunar peak at 1857.2. To become completely out of phase, a difference of 0.2 years/cycle (i.e., a period of 9.1 or 9.5 years) takes about 23 cycles (or about 214 years) and a difference of 0.1 years/cycle (i.e., a period of 9.2 or 9.4 years) takes about 46 cycles (or about 428 years); sufficient data are not available to evaluate either of these cases.

For over 150 years, reported years of peak abundance of Ruffed Grouse and Snowshoe Hare have persistently stayed in phase with predicted peak years based on the lunar model $P_n = 1950.22 \pm 9.3n$ (Archibald 1977), differing by an average of 0.9 years (Table 1). Differences between mean reported and predicted peak years appear to have become larger after about 1965, with the reported peaks consistently lagging behind the predicted peaks.

9.3-year lunar declination cycle

The 9.3-year cycle in the maximum lunar declination from the ecliptic in absolute value at the equinoxes is shown in Figure 1. The alternating higher declination peaks are years when the moon's maximum declination runs below the ecliptic. Semidiurnal (result in two high tides and two low tides per day) and diurnal (result in one high and one low tide per day) tidal factors oscillate in 18.6-year cycles, 180° out of phase, with diurnal factors largest when lunar declination is highest (1950, 1968, 1987, 2006) and semidiurnal factors highest when lunar declination is minimal (1959, 1978, 1997) (McKinnell and Crawford 2007). The semidiurnal lunar forces are 23% less when the moon reaches its maximum declination of 28.6°. The solar semidiurnal forces are reduced by 16% when the sun is at its maximum declination of 23.5° at the solstices (Pugh 1996). To sum up, tidal forces reach a maximum when the moon is in the equatorial plane (i.e., at zero declination from the ecliptic), which happens twice during the 18.6-year nodal cycle or every 9.3 years.

9.3-year moonlight cycle

The full moon can be above the horizon both before dusk and after dawn the following morning, resulting in a "night without darkness" with light levels no lower than full moonlight. This can occur on two successive nights and in several months in a row. The nodal cycle causes an 18.6-year cycle of total minutes that the full moon is above the horizon both before dusk and after the following dawn at the full moon nearest the autumnal equinox (light bars in Figure 1). The westward regression of the lunar nodes from the autumnal equinox to the vernal equinox takes 9.3 years. Then, there is a corresponding 18.6-year cycle of total minutes that the full moon is above the horizon both before dusk and

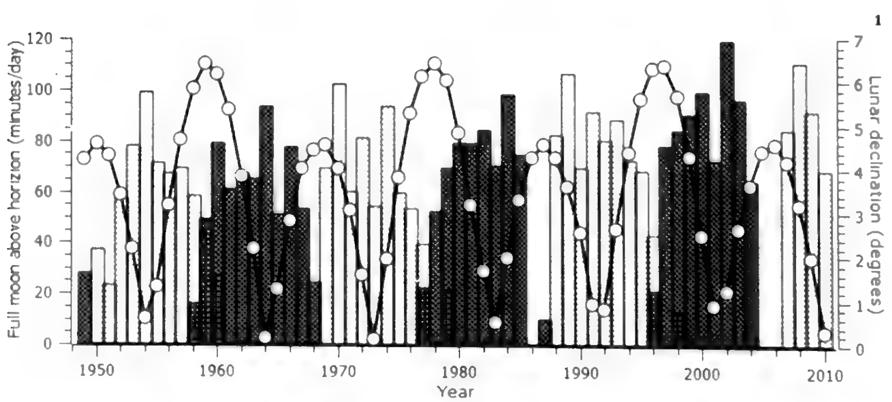

FIGURE 1. Length of time full moon (April, dark shading; September, light shading) was above the horizon both before dusk and after the following dawn (total minutes/day) and maximum lunar declination (open circles) in September relative to the ecliptic in absolute value (50°N, 90°W).

after the following dawn during the full moon nearest the vernal equinox (dark bars in Figure 1). Therefore, this phenomenon occurs every 9.3 years, alternating between the vernal and autumnal equinoxes. Nights without darkness occur multiple times in the years at or near the peak of the cycle. For example, in the September peak year 1991, there were nine nights without darkness: July 26, August 24–25, September 23–24, October 22–23, November 21, and December 20. Although the midnight sun near the summer solstice at higher latitudes is well known, there appears to be nothing in the literature about this nights-without-darkness phenomenon at the equinoxes. The only information I have found so far about "sun and full moon both up" are some anecdotal reports of confused homing pigeons flying in the wrong direction, perhaps because they mistook the rising full moon for the sun. The 9.3-year moonlight cycle is inversely related to the 9.3-year lunar declination cycle (Figure 1).

Correlations with 10-year wildlife population cycles

Ruffed Grouse drumming counts in Minnesota are positively correlated ($r^2 = 0.26$, $P < 0.001$, with 1-year lag) with September maximum lunar declination (Figure 2) and, therefore, inversely related to the moon's tidal force. During the equinox months of September and March, full and new moons always coincide with minimum lunar declination (moon over the earth's equator) (Brahde 1988). There is some tendency for grouse peaks to alternate in amplitude (i.e., every other peak is a "high" peak) (Archibald 1977). High grouse peaks are associated with years when the moon's maximum declination runs *above* the ecliptic. Because the zeitgeber effect of the 9.3-year nodal half-cycle "need not occur in more than 2 3 consecutive years per decade" (Archibald 1977), interpretation of correlation coefficients (which cover all years) is problematic.

Snowshoe Hare density in the Yukon Territory is also directly correlated ($r^2 = 0.41$, $P < 0.001$, with 2-year lag) with September maximum lunar declination and inversely correlated with the moon's tidal force (Figure 3). There is also a tendency for hare population peaks to alternate in amplitude (Archibald 1977); higher peaks coincide with years when the moon's maximum declination runs *below* the ecliptic.

2

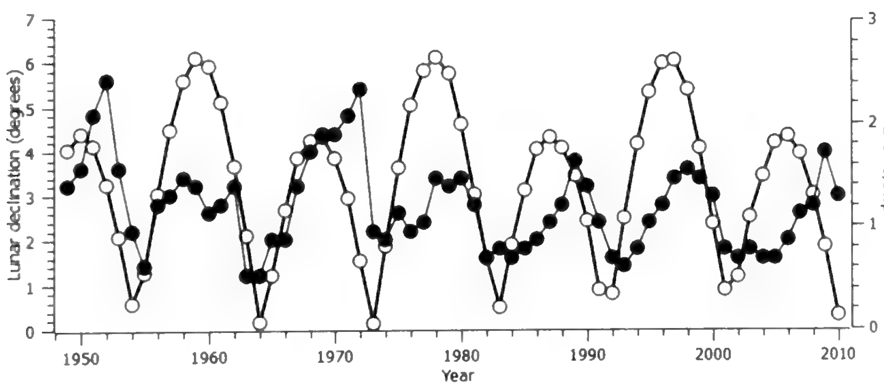

FIGURE 2. Maximum lunar declination (open circles) in September relative to the ecliptic in absolute value (50°N, 90°W) compared with spring drumming counts (closed circles) for Ruffed Grouse (*Bonasa umbellus*) in Minnesota, 1949 2010 (Minnesota DNR).

3

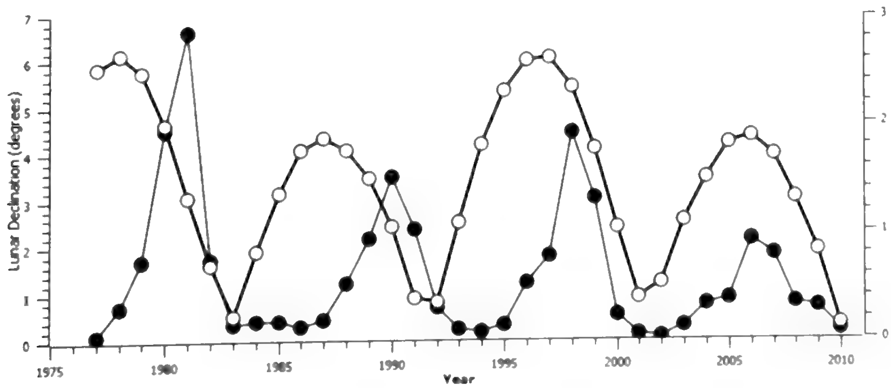

FIGURE 3. Maximum lunar declination in September (open circles) relative to the ecliptic in absolute value (50°N, 90°W) compared with spring Snowshoe Hare (*Lepus americanus*) density (closed circles) in the Kluane region of the Yukon Territory, 1977–2010 (Krebs 2011).

The cyclic nights-without-darkness phenomenon at the equinoxes generally starts to increase 1–2 years before the Snowshoe Hare peak; it peaks during the hare decline and stays relatively high throughout the hares' low phase (Figure 4). The inverse relation between Snowshoe Hare density and nights without darkness during the low phase is intriguing because explanation of the low phase remains a puzzle (Krebs *et al.* 2001). Similar to hare density, nights without darkness generally increase following an increase in Ruffed Grouse density and stay relatively high during the ensuing low (Figure 5).

Ruffed Grouse population model

The following model of Ruffed Grouse drumming is based on a single exogenous factor, the nodal cycle of the moon:

$$\text{Drums/stop}(t) = 1.27 + 0.55\sin(2\pi\ )/9.307 * (t-1) + 1.41) + 0.55\sin(2\pi\ )/18.6134 * (t-1) + 0.90\pi)$$

Where t is the year (yyyy) with 1-year lag; 9.307 and 1.41 are the period and phase angle of the nodal phase cycle, respectively; 18.6134 and 0.90 are the period and phase angle of the nodal amplitude cycle (Yndestad 2009); 1.27 is the amplitude; and 0.55 is half the range of observed Minnesota drumming counts.

The model output matches the observed Ruffed Grouse cycle fairly well ($r^2 = 0.39$, $P < 0.001$), in both period and alternating amplitude (Figure 6).

Canada Lynx population model

$$\text{Furs/year}(t) = 20800 + 16540\sin(2\pi\ /9.307 * t + 1.41\pi) + 16540\sin(2\pi\ /18.6134 * (t-9.307) + 0.90\pi\ )$$

Where t is the year (yyyy) with no lag on the 9.3-year phase cycle and a lag of 9.307 years on the 18.6-year amplitude cycle (to offset the higher peaks); 9.307 and 1.41 are the period and phase angle of the nodal phase cycle, respectively; 18.6134 and 0.90 are the period and phase angle of the nodal amplitude cycle (Yndestad 2009), 20800 is the amplitude and 16540 is half the range of observed Northern Department lynx fur returns between 1842 and 1918 (Elton and Nicholson 1942).

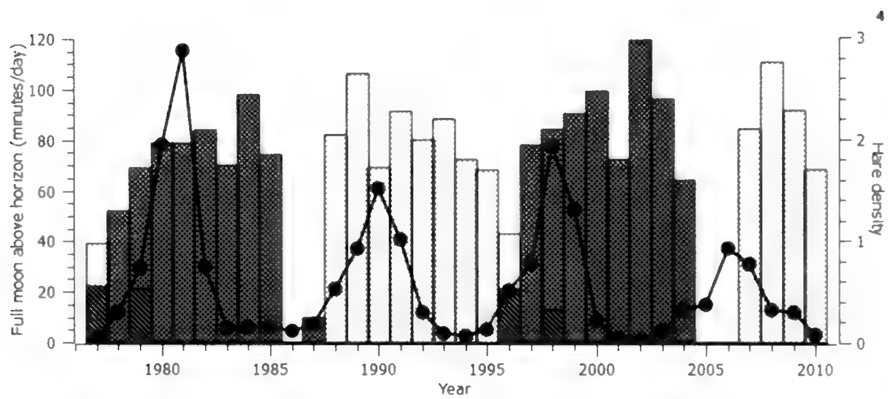

FIGURE 4. Length of time full moon (April, dark shading; September, light shading) was above the horizon both before dusk and after the following dawn (total minutes/day; 50°N, 90°W) compared with spring Snowshoe Hare (*Lepus americanus*) density (closed circles) in the Kluane region of the Yukon Territory, 1977–2010 (Krebs, 2011).

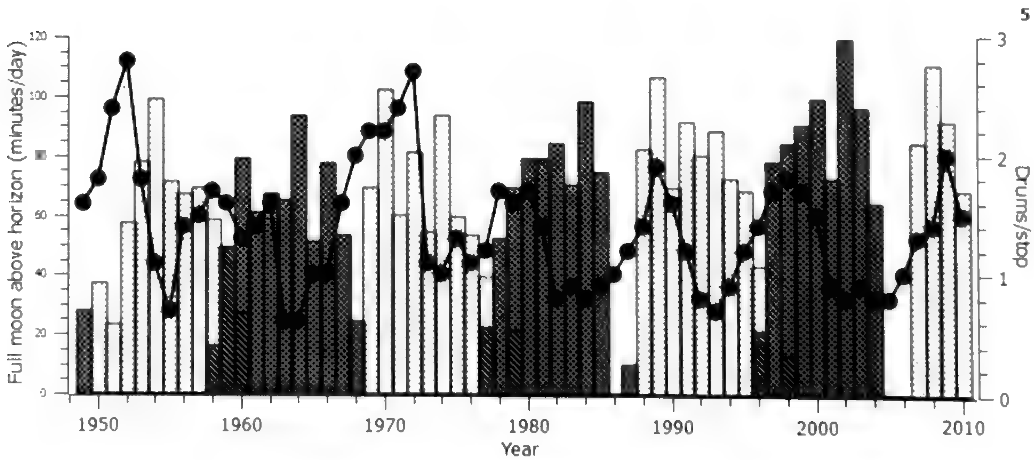

FIGURE 5. Length of time full moon (April, dark shading; September, light shading) was above the horizon both before dusk and after the following dawn (total minutes/day; 50°N, 90°W) compared with spring drumming counts (closed circles) for Ruffed Grouse (*Bonasa umbellus*) in Minnesota, 1949–2010 (Minnesota DNR 2011).

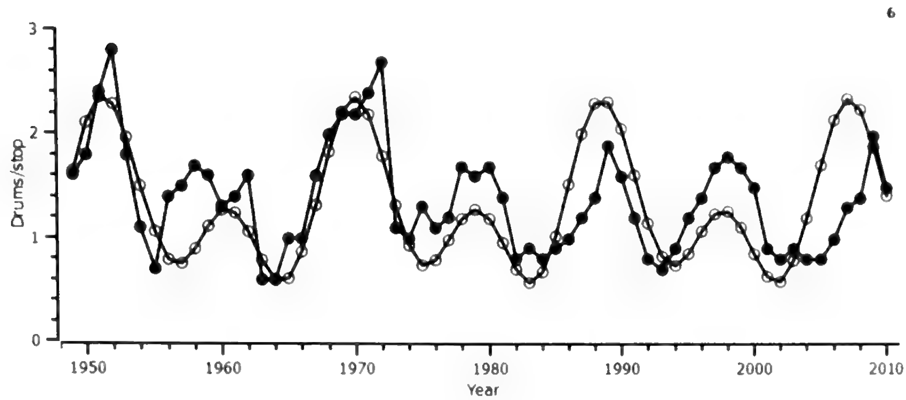

FIGURE 6. Spring drumming counts (open circles) predicted by the lunar model compared with observed drumming counts (closed circles) for Ruffed Grouse (*Bonasa umbellus*) in Minnesota, 1949–2010 (Minnesota DNR 2011).

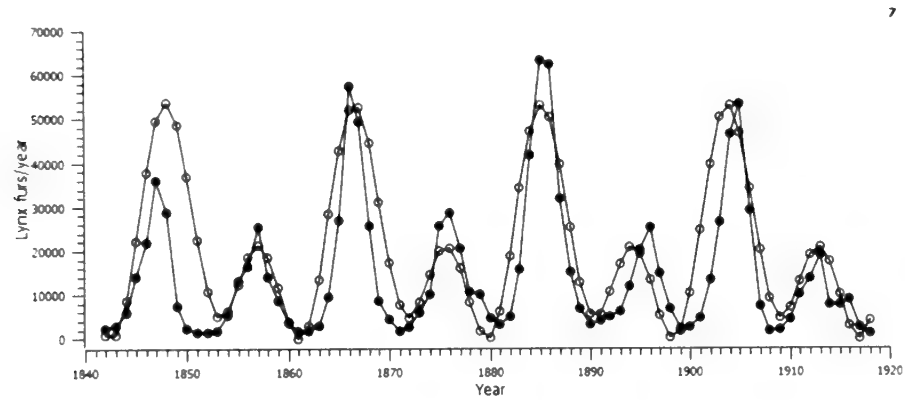

FIGURE 7. Canada Lynx (*Lynx canadensis*) fur returns predicted by lunar model (open circles) compared with observed Canada Lynx fur returns (closed circles), Northern Department, 1842–1918 (Elton and Nicholson 1942).

The model output matches the "classic" Canada Lynx cycle quite well ($r^2 = 0.62$, $P < 0.001$) in both period and alternating amplitude over the period 1842–1918 (Figure 7). Note that additional decimal places in the period values were used in the Rugged Grouse and Canada Lynx population models because the formulas are very sensitive to small differences in period length.

Discussion

Key cycle features accounted for

King and Schaffer (2001) list five important features of the 10-year wildlife cycle, and a definitive explanation for the cycle should account for all five points. The 9.3-year half period of the nodal cycle hypothesis provides a plausible explanation of each of these five features:

1. *Regularity:* Reported peak population years have stayed in phase with predicted peaks based on the 9.3-year lunar cycle for over 150 years (Table 1).
2. *Period:* The overall mean cycle period (9.4 years) is close to the 9.3-year period of the lunar cycle (Table 1).
3. *Amplitude:* Peaks in the Snowshoe Hare cycle tend to alternate in amplitude (Archibald 1977). The trend is evident in the Hudson's Bay data from 1857 to 1896 (MacLulich 1957) and a century later at Kluane Lake (Figure 3). Schaffer (1984) noted alternating amplitude in the Canada Lynx cycle from 1821–1913. Higher peaks in the hare-lynx cycle are associated with vernal equinox peaks in the lunar cycle (Figure 4) and maximal semidiurnal tidal factors. Ruffed Grouse peaks also tend to alternate in amplitude but higher peaks in the grouse cycle are associated with autumnal equinox peaks in the lunar cycle (Figure 5), when the moon's maximum declination runs above the ecliptic (Figure 2) and diurnal tidal factors are largest.
4. *Distribution:* The 10-year cycle is a northern phenomenon restricted to latitudes above 45–50°N in North America (Archibald 1977) and even higher latitudes in northern Europe. Northern populations of Snowshoe Hares and Ruffed Grouse are cyclic, while more southerly populations exhibit little or no periodicity (Rusch 1989; Murray 2003). Several effects of the lunar nodal cycle increase significantly with latitude. For example, the full moon was above the horizon at both dusk and dawn on the night of April 29–30,

1999, for a total of 71 minutes at 40°N, 90 minutes at 50°N and 131 minutes at 60°N. Latitude is an important factor governing both the species (semidiurnal and diurnal) and maximum amplitude of tides (Pugh 1996).

5. *Synchrony:* Regional synchrony of populations over wide geographic areas has been reported for both Snowshoe Hare and Ruffed Grouse (Keith 1963), and population levels of these species tend to be closely aligned within the same areas, with peaks predominantly 1 year apart (Keith 1963). Selas (2006) found transatlantic synchrony in Snowshoe Hare/Mountain Hare (*Lepus timidus*) and Canada Lynx/Eurasian Lynx (*Lynx lynx*) series, suggesting that the cycles are triggered by a common large-scale phenomenon. Synchrony is to be expected under a lunar cycle hypothesis, because lunar phenomena, such as height in the sky, rise and set times, and gravitational pull are similar worldwide at a given latitude, varying only because of such factors as elevation and topography.

Population modeling

King and Schaffer (2001) developed a tri-trophic population dynamics model of the Snowshoe Hare cycle with browse, hare, and predator density as dependent variables and 14 parameters (but no weather factors). They concluded that the increase phase is halted by food limitation and the decline from peak numbers is due to predation. Yan *et al.* (2013) used two-level population models with rate of change of hare and lynx as dependent variables and either global weather indices or local temperature, rainfall, and snowfall with various time lags. Their simulations showed that predation and direct, as well as delayed, density dependency are necessary, but not sufficient, factors for the appearance of 10-year hare–lynx cycles and that external climatic forcing through rainfall and snowfall are essential to produce 10-year cycles.

Zimmerman *et al.* (2008) used comparative model selection to assess the correlation of numerous combinations of 13 hypothesized factors with spring drumming counts for grouse in northeastern Minnesota over a 22-year period. The hypothesized factors included goshawk abundance (predation), Eastern Tent Caterpillar (*Malacosoma americanum* [Fabricius, 1793]) abundance (aspen defoliation), weather during the breeding season, weather during the previous winter, colour phase ratios (phenotypic hypothesis), fall age ratios (recruitment), and male grouse weight (condition entering winter). The best model indicated that grouse abundance was highest during cold snowy and warm dry winters, presumably related to optimal snow-roosting conditions during periods of extreme cold. As the best model accounted for only 17% of the variation in drumming counts, these authors concluded that several interacting factors most likely cause the cycle but the mechanism remains unknown.

Using a multiple regression model, Selas (2014) found that a maximum September lunar declination index (3-year lag), March–April North Atlantic Oscillation, previous August–October North Atlantic Oscillation and sunspot numbers accounted for 38% of the variation in an Autumnal Moth index from Fennoscandia covering 113 years. A similar model, which used the Pacific–North American index instead of the North Atlantic Oscillation, accounted for 23% of the variation in a Canada Lynx population index for the period 1950–2009.

The Canada Lynx model presented here, with just the 9.3- and 18.6-year lunar parameters, accounted for 62% of the variation in the Northern Department fur returns over 77 years (Figure 7). The Ruffed Grouse model presented here accounted for 37% of the variation in the Minnesota Ruffed Grouse drumming counts over 62 years (Figure 6). This suggests that *both* the 9.3-year and 18.6-year nodal cycles play a significant role in lynx and grouse population dynamics. A prediction model with four lunar parameters including *both* the 9.3 and 18.6-year nodal periods accounted for 62% of the variation in strong-to-violent March–August tornadoes in the United States between 1950 and 2012 (Eppelbaum 2013). Schaffer's (1984) power spectrum analysis of Canada Lynx fur returns (1821–1913) showed a fundamental period of roughly 10 years and a second harmonic period of about 20 years. The obvious similarity in periods suggests that the "underlying determinism" this author sought could well be the 18.6-year nodal cycle and its 9.3-year sub-harmonic. Further research directed toward gaining an understanding of the interaction of the 9.3-year and 18.6-year nodal cycles is clearly needed. Also apparent from these model results is that, while density-dependence may well play a part in nature and is a critical component of prevailing models of cyclic populations, it is not necessary to closely mimic the cyclic population dynamics of the Canada Lynx and Ruffed Grouse.

Spatial synchrony

Regional synchrony is expected under a lunar hypothesis, and the problem to be reconciled is why the synchrony is not absolute (Krebs *et al.* 2001). Some asynchrony can be expected between even nearby populations because of differences in local conditions. Selas (2006) suggested that spatial asynchrony in hare cycles could result from asynchronous fluctuations in plant chemistry due to regional variations in UVB levels caused by differences in cloud formation or ozone distribution. If the zeitgeber effect of the lunar nodal half-cycle occurs for 3–4 years at the bottom of the cycle, more regional variation in the timing of the subsequent peak would be expected because of differences in local environmental conditions and food webs. But this explanation does not account for the tendency for synchrony of Snowshoe Hare populations to spread out from a north-central Canada in traveling waves.

Smith (1983) found that peaks in the Snowshoe Hare cycle began in a central Canada core area (Saskatchewan and Manitoba) and traveled outward in waves with 1-year and then 2-year phase lags in the peak year occurring with increasing distance. Selas (2014) found that the increasing phase lag of Canada Lynx population peaks moving away from the core area was significantly negatively related to cosmic radiation levels. In other words, Canada Lynx tend to peak first in areas of highest radiation (i.e. the "core area of the auroral oval"). Although it may be a contributing factor, the cosmic ray hypothesis seems an unlikely overall explanation for a metronomic population cycle because, first, the 9.3-year lunar cycle and the 11.1-year solar cycle will go completely in and out of phase every 103 years and, second, Selas found that the solar signal had a much stronger relation to geomagnetic activity than the lunar signal.

The earlier peaking in the core area could be due to the generally flatter topography of central Canada if the lunar zeitgeber effect on the Snowshoe Hare involves nights without darkness. The shadow effect of mountainous and hilly terrain can be expected to produce later actual rise and earlier actual set times resulting in nights without darkness occurring in fewer consecutive years (hence the lags) and with less biological impact.

Regarding the search for a mechanism, one initial question that arises is whether there is a single mechanism underlying all 10-year wildlife population cycles. Several observations suggest not. The 9.3-year cycles of the Autumnal Moth in Fennoscandia and the Douglas Fir Tussock Moth (*Orgyia pseudotsugata* [McDunnough, 1921]) in the Pacific Northwest are almost completely out of phase with the Snowshoe Hare and Ruffed Grouse cycles in North America (Archibald, unpublished data; Selas 2014), strongly suggesting a different mechanism. Also, the difference in peak amplitude alternation between the Snowshoe Hare and Ruffed Grouse cycles could result from a different mechanism.

"Correlation means little unless we see a plausible causal relationship" (Royama 1992). The two 9.3-year lunar cycles reported here provide the basis for speculative mechanistic explanations of the 10-year wildlife cycle. Other 9.3-year cycles resulting from the nodal cycle may await discovery. The 9.3-year moonlight cycle could have behavioural, physiological, chronobiological, or phenological effects. The 9.3-year declination cycle could have an impact on cyclic population dynamics through effects of oceanic and atmospheric tides on climatic factors, such as cloudiness and UVB and cosmic radiation, which, in turn, affect food plant quality.

Ruffed Grouse population peaks tend to follow maximum lunar declination by 1–2 years (Figure 2). And grouse lows are closely associated with minimum lunar declination, suggesting that the declination effect could be on food quality or palatability rather than directly on the grouse itself. The primary winter food of northern Ruffed Grouse is Trembling Aspen (*Populus tremuloides* Michaux) buds and aspen use is correlated with Ruffed Grouse density (Jakubas and Gullion 1991). These authors found that Ruffed Grouse consistently selected Trembling Aspen buds with relatively low levels of coniferyl benzoate and that high levels of this secondary metabolite were associated with declining or low grouse density. Captive Ruffed Grouse assimilated 24% less energy from aspen buds with high levels of coniferyl benzoate (Guglielmo *et al.* 1996). Jakubas and Gullion (1991) concluded that the impact of a shortage of suitable aspen in winter "may increase predation risks and energetic costs for Ruffed Grouse." It is interesting that, during four winters between 1985 and 1990, the coniferyl benzoate levels Jakubas and Gullion reported were highly correlated ($r^2 = 0.84$) with lunar declination.

Cloud conditions have more impact in terms of attenuating UVB radiation than stratospheric ozone, particularly at high latitudes (Svenoe *et al.* 1995). Pertsev and Dalin (2010) separated lunar-phase and lunar-declination effects on cloudiness; both were statistically significant with lunar declination somewhat stronger. They found a semi-monthly (13.66-day) variation in tropospheric nighttime cloudiness, with the relative amount of cloud increasing with an increase in lunar declination by absolute value. If this relation is extendable (Ray 2007) from the fortnightly half-period of the nodical month to the 9.3-year half-period of the nodal cycle, the maximum declination line in Figure 2 may also represent relative cloudiness. If so, then Ruffed Grouse density is correlated with attenuation of UVB radiation, which is generally thought to have a positive effect on food quality (van Asch and Visser 2007). The relation is particularly apparent at the Ruffed Grouse's cyclic lows, when exposure of food plants to UVB light is highest. Ayres (1993) linked reduced radiation resulting from increased cloud cover to reduced (average of 54%) secondary metabolites in food plants and their increased palatability to herbivores. In one study, Snowshoe Hares showed a strong preference for shaded Alaska Paper Birch (*Betula papyrifera* ssp. *humilis* [Regel] Hultén) shoots (Bryant *et al.* 1987). The mechanistic pathway suggested here is: increased lunar declination leads to increased cloudiness resulting in reduced UVB radiation and reduced secondary metabolites leading to increased herbivore use and higher herbivore density. This scenario is similar to the UVB plant stress hypothesis proposed by Selas (2006) as a possible cause of the Snowshoe Hare cycle, except that the driving force here is the 9.3-year lunar nodal cycle rather than the 11.1-year sunspot cycle and the intermediary is cloudiness rather than ozone.

Snowshoe Hare population peaks tend to precede maximum lunar declination by 1–2 years, and increasing hare abundance is closely aligned with increasing lunar declination (Figure 4). Like grouse, hare population lows are associated with minimum lunar decli-

nation, suggesting that maximum tidal force is detrimental, directly or indirectly, to both species. Sinclair *et al.* (1988) rejected a "fluctuating secondary compound hypothesis" to explain the Snowshoe Hare cycle because phenols declined through the increase and decline phases and increased during the low phase — exactly the opposite of what was predicted. Boonstra *et al.* (1998) posited that the low phase of the hare cycle might be related to deterioration in food quality because of the production of secondary plant defense compounds but dismissed this idea because of the failure of the fluctuating secondary compound hypothesis .

However, suppose that lower lunar declination (maximum tidal force) somehow raises the level of secondary metabolites in food plants above the threshold that the hare must stay beneath in order to grow, reproduce, and survive. In this case, the low phase of the hare cycle would continue until the lunar declination increases enough to exceed the threshold. Further study may clarify this issue.

The relative timing of the 9.3-year moonlight cycle and Snowshoe Hare density (Figure 4) suggests a possible mechanism for the Snowshoe Hare cycle, i.e., nights without darkness at the equinoxes produce a cyclic acceleration of the effects of key factors affecting the hare cycle: predation rate, predation risk, predator-induced stress, and nutritional deficiency. Predation is generally considered to be the driving factor in the hare cycle (Murray 2003). The rate of predation on Snowshoe Hares is higher when the moon is full (Griffin *et al.* 2005). Griffin and Mills (2009) found that weekly hare survival rates were about 2% lower in spring and fall compared with summer and winter rates. Spring and fall are the seasons when there is a possibility of a pelage–background colour mismatch resulting in heightened vulnerability to predation (Litvaitis 1991). The increased duration of moonlight near the peak of the 9.3-year lunar cycle can be expected to increase the time of elevated predation risk. Lima and Bednekoff (1999) suggested that animals should exhibit the greatest antipredator behaviour in high-risk situations that are brief and infrequent. Snowshoe Hares forage almost exclusively in twilight and at night (Griffin *et al.* 2005). Lack of darkness after sunset could result in either delayed feeding or foraging restricted to areas of protective cover but lower quality food. In either case, the resulting reduced food intake may lead to declining body condition and reduced reproductive output (Boonstra *et al.* 1998). Rongstad and Tester (1971) found that the 5–10-minute daily return of Snowshoe Hares to care for their young appeared to be related to light intensity in the evening twilight period; this behaviour so crucial to juvenile survival could be affected by nights without darkness. Chronic predator-induced stress has been posited to decrease reproductive fitness during the peak and decline phases of the hare cycle (Boonstra *et al.* 1998; Krebs *et al.* 2001; Sheriff *et al.* 2010). Nights without darkness may contribute to increased stress due to conflict between predator avoidance and hunger.

The cyclic predation acceleration mechanism suggested for Snowshoe Hares may also be applicable to the Ruffed Grouse cycle (cf. Figures 4 and 5). In a large study of radio-marked grouse in northwestern Wisconsin, Lauten (1995) found that 96% of 341 known mortalities were due to predation or hunting. Bumann (2002) reported the highest predation rates in September, March, and April. Spring and fall are dangerous seasons for Ruffed Grouse; behaviour such as drumming, territorial defense, nesting, and dispersal are likely to increase predation risk at the same time that raptors are migrating. Rusch and Keith (1971) found that predation of adult males was highest during the spring and fall drumming periods. Archibald (1976) reported that moonlight was the major external factor stimulating drumming and found that nearly continuous nocturnal drumming occurred around the full moon in April. From fall to spring, however, Ruffed Grouse activity is highly crepuscular. Archibald (1973) found that late winter activity, which consisted mainly of travel to and from and feeding in aspen clones, peaked about 30 minutes before sunrise and almost precisely at sunset. Lack of darkness after sunset and before sunrise on nights without darkness could disrupt the timing, location, or duration of feeding resulting in nutritional deficiency, increased predation risk, or perhaps stress.

The lunar nodal cycle could also affect cyclic population dynamics through a cyclic impact on phenology. Temperature and photoperiod are the two most important phenological factors (van Asch and Visser 2007), and the lunar nodal cycle may play a role in both cases. First, cyclic nights without darkness at the equinoxes could confuse the perception of photoperiod. Bunning and Moser (1969) suggested that moonlight might interfere with photoperiodic time measurement in some plants and animals. Bowden (1973) posited that periods of continuous illumination at full moon could provide photoperiodic cues for insects. Interruptions in normal circadian light cycles and the resulting disruption of normal melatonin rhythms cause widespread effects involving reproduction, physiology, and behaviour (Navara and Nelson 2007). If nights without darkness at the equinoxes disrupt the circadian rhythms of Snowshoe Hares, there are several possible effects including timing of reproductive processes and molt. Change in day length is most rapid near the equinoxes and increases with latitude (e.g., ~5.5 minutes/day at 60°).

Second, there is growing evidence that climatic factors are influenced by the lunar nodal cycle. The surface climate of much of western and central Canada is strongly influenced by a large-scale atmospheric variation, the Pacific–North American (PNA) teleconnection (Mysterud *et al.* 2003). McKinnell and Crawford (2007) reported that the PNA index accounted for over

70% of the variation in average air temperature at and near Sitka, Alaska, in January. In addition, they found that the PNA index was significantly negatively correlated with the lunar nodal cycle with a 2-year lag. Yndestad (2006) found that the North Atlantic Oscillation winter index was correlated with the lunar nodal cycle. Meslow and Keith (1971) found that the onset of breeding in Snowshoe Hares was significantly correlated with the intensity of illumination (measured by cloud cover) during the previous midwinter. Major seasonal molts (which occur near the equinoxes) in the Snowshoe Hare are controlled by photoperiod (Murray 2003), whereas snow onset and disappearance are governed by temperature (Kielland *et al.* 2010). Because the nodal cycle may have a cyclic influence on both factors, there is an interesting possibility that the degree of pelage–background colour asynchrony from year to year may be cyclic as well. The lunar nodal cycle could conceivably affect Ruffed Grouse phenology through an effect on the timing of drumming, mating, or dispersal as well as the synchrony of hatching and chick food availability.

Recent research suggests that lunar declination may be an important factor in the ecology of northern latitudes. Ramos da Silva and Avissar (2005) found that the Arctic Oscillation has been "unambiguously correlated" with the 9.3- and 18.6-year oscillations of the lunar nodal cycle since the 1960s. Yasuda (2009) found a statistically significant 18.6-year periodicity, synchronized with the nodal cycle, in tree-ring chronologies in western North America over a 300-year period, and attributed this bi-decadal variability to tidal mixing. Several authors have reported 13.66-day (fortnightly) oscillations in Arctic tidal mixing, with maximum heat flux occurring at minimum lunar declination (Rogachev *et al.* 2001; Martin *et al.* 2004). According to Ray (2007), "the tidal mixing mechanism so plainly evident at near-fortnightly periods should extend in principle to the 18.6-year period." Li *et al.* (2011) found 13.6-day and 27.3-day oscillations in atmospheric pressure fields and atmospheric geopotential height (which is what climatic indices such as the PNA teleconnection and the North Atlantic Oscillation measure). The lunar forcing of these atmospheric tides reaches its maximum when the lunar declination is zero. Krahenbuhl *et al.* (2011) reported that the 27.3-day maximum lunar declination cycle influences upper tropospheric circulation by deforming high latitude Rossby waves, which are associated with the formation of weather systems. Foreman *et al.* (2006) estimated that the 18.6-year nodal modulation causes a 19% variation in the net incoming tidal energy flux of the Bering Sea basin. The 18.6-year lunar nodal cycle accounted for 59% of the variance in Pacific Halibut (*Hippoglossus stenolepsis*) recruitment from 1927 to 1983 (Parker *et al.* 1995). Based on wavelet analysis, Yndestad (2009) concluded that the biomass variability of zooplankton, capelin, cod, and herring in the Barents Sea was related to both the 18.6-year amplitude and the 9.3-year phase tide. So it seems possible that the climatic forcing that Yan *et al.* (2013) found necessary for successful modeling of the Canada Lynx cycle was actually the effect of the underlying lunar nodal cycle.

There is some evidence that the 10-year wildlife cycle has changed in recent years. Krebs *et al.* (2013) reported that the widespread regional synchrony of hare and lynx populations found in northwestern North America from 1970 to 1990 broke down after the mid-1990s. These authors found that Canada Lynx populations peaked in the early 1970s, 1980–81 and 1989–91, but there was no clear sign of a strong cyclic lynx peak after 1995. This study shows substantially greater differences between predicted and mean reported peak years after about 1965 (Table 1). Long-term monitoring of 10-year-cycle species is required to increase our understanding of cyclic phenomena (Krebs *et al.* 2013) and to assess possible links between changes in population cycles and global warming (Yan *et al.* (2013).

Just a coincidence?

Some ecologists will contend that the correlations presented here are merely a coincidence. The coincidence involves not only period but also phase: peaks of the Snowshoe Hare and Ruffed Grouse cycles are aligned with peaks of the nodal half-cycle. Period, phase, and amplitude of the Ruffed Grouse cycle in Minnesota and the "classic" Canada Lynx cycle in northern Canada can be mimicked by the lunar models presented. One school of ecological thought holds that experiments are the only way to separate causation from spurious correlation (Lambin *et al.* 2002). Unfortunately, the 9.3-year moonlight and lunar declination cycles are not subject to experimental manipulation in the field. Moreover, there does not appear to be any statistical method available to prove that the 9.3-year nodal half-cycle actually causes the timing of the 10-year cycle (Lindstrom *et al.* 1996; Berryman 2002). However, without invoking an exogenous zeitgeber, the persistent period, regularity, and synchrony of the 10-year cycle are difficult to explain convincingly. The 9.3-year moonlight cycle and 9.3-year lunar declination cycle are plausible causative factors. Previously, it was stated that the ideal exogenous factor candidate would have a consistent period that matched the wildlife cycle and would shed light on its other unexplained features. The 9.3-year nodal half-cycle of the moon meets these criteria. Unlike sunspots, the wildlife cycle has stayed in phase with the nodal half-cycle for 150 years despite major disruptive influences (e.g., Krakatoa) that might be expected to "affect the future course of the cycle and thus become incorporated into the future history of the series" (Moran 1953).

Acknowledgements

Thanks to Vidar Selas for advice and encouragement, and to Marlene Klemm for interlibrary loans. I am indebted to Duncan MacLulich, Charles Elton,

Lloyd Keith, the Minnesota DNR, Charles Krebs and their many colleagues for supplying the long-term data series that are the foundation of this paper. This work would not have been possible without the free tools available on the internet including the Astronomical Sky Calendar, Google Scholar, JPL Horizons, US Naval Observatory, and Wessa Statistics Software.

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Received 1 February 2012
Accepted 8 June 2013

Habitat Selection and Nest Success of the Upland Sandpiper (*Bartramia longicauda*) in Ivvavik National Park, Yukon, Canada

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Miller, Valerie, Erica Nol, Linh P. Nguyen, and Devin M. Turner. 2014. Habitat selection and nest success of the Upland Sandpiper (*Bartramia longicauda*) in Ivvavik National Park, Yukon, Canada. Canadian Field-Naturalist 128(4): 341–349.

The Upland Sandpiper (*Bartramia longicauda*) is a grassland shorebird species associated primarily with prairie habitats in central North America. A disjunct and poorly studied population also occurs in Yukon, Canada, and Alaska, United States. We studied habitat selection of nesting Upland Sandpipers in Ivvavik National Park, Yukon, at the scales of microhabitat (1-m radius around nest) and putative home range (11.3-m radius plots at nests and within 50 m of nest). At the microhabitat scale, the Upland Sandpiper selected nest sites with lower visibility from above than that of their home range (median 91.5%, range 70–98% versus median 99.0%, range 85–100%) and less-variable composition of vegetation than at random sites within the home range. Vegetation adjacent to the nest in the eastern quadrat was significantly shorter (mean ± standard error: 10.6 ± 1.55 cm) than that in other directions around the nest (> 13 cm); nest sites and microsites within home ranges were more often hummocky than random sites in the park. At the mesohabitat scale, Upland Sandpipers selected sites within home ranges with fewer trees than random sites within the park (10.3 ± 3.0 trees per 11.3-m-radius plot around nest versus 32.9 ± 5.9 trees per 11.3-m-radius plot in the park) and greater herbaceous cover (70.7% ± 3.0% versus 56.2% ± 3.7%). Despite the disproportionate use of sites with fewer trees, more herbaceous cover, and lower vertical visibility, these factors did not relate to nest success in our sample. Of the 24 nests found in 2010 and 2011, 22 contained four eggs and 2 contained three eggs. Upland Sandpipers at this high latitude site had a nesting success rate of 0.85 ± 0.01 and 0.56 ± 0.01 in 2010 and 2011, respectively, for a 21-day incubation period. Further assessment of the selected characteristics of nesting sites will improve our ability to predict the effects of northward shrub and tree encroachment on this grassland species.

Key Words: Upland Sandpiper; *Bartramia longicauda*; mesohabitat; microhabitat; nest-site selection; northern limit; shorebirds; Yukon; Ivvavik National Park

Introduction

Habitat selection refers to the preference of specific environmental attributes that differ from other sites to enhance fitness, survival, or both (Block and Brennan 1993; Jones 2001). Nest-site selection is a top-down, hierarchical process that begins at the regional scale followed by home range then specific nest site (Block and Brennan 1993; Jones 2001). Vegetation characteristics are typically important features of nest-site selection for birds (Rodrigues 1994; Bollinger 1995; Clark and Shutler 1999).

We studied vegetation characteristics that may influence nest-site selection by the Upland Sandpiper (*Bartramia longicauda*), a medium-sized, grassland-nesting shorebird. The largest part of the geographic range of the Upland Sandpiper is in the Great Plains of North America, although several small, disjunct populations occur in northwestern Canada and Alaska (Houston *et al.* 2011). In the central and southern part of its breeding range, the Upland Sandpiper prefers to nest in large open grasslands with flowering herbaceous vegetation and avoids woody and tall, dense vegetation (Kirsch and Higgins 1976; Ailes 1980; Bowen and Kruse 1993; Vickery *et al.* 1994; Dechant *et al.* 2003*). Despite some early publications on this species (Buss 1951; Campbell 1967), there has been a near absence of recent research from the northern disjunct range (Nouvet *et al.* 2008), where warmer temperatures, earlier springs, and longer growing seasons associated with climate change have resulted in the advancement of the treeline (Szeicz and Macdonald 1995; Sturm *et al.* 2001; Moen *et al.* 2004).

The objectives of our study were to describe the characteristics of the habitat surrounding nest sites at the microhabitat scale and within a 50-m radius, the presumed home range of the Upland Sandpiper (Mong 2005) and to compare habitat characteristics of successful and unsuccessful nests at appropriate scales. Based on nesting habitat characteristics described for southern populations (Kirsch and Higgins 1976; Ailes 1980; Bowen and Kruse 1993; Bollinger 1995; Dechant *et al.* 2003*; Vickery *et al.* 2010*), we predicted that the Upland Sandpiper would select home ranges and nest sites in open, grassland areas with little woody cover. We also predicted that parents with nests closer to trees, more trees in the home range, and less vertical nest cover would experience less reproductive success than those with nests farther from trees, fewer trees in the home range, and more vertical nest cover. Our final objective was to document nest survival of the Upland Sandpiper in the disjunct northern population for com-

parison with other studies from the centre of its breeding range.

Study Area

We collected data within a 4-km^2 area surrounding Sheep Creek (69°09'N, 140°09'W) in Ivvavik National Park, Yukon, Canada. Sheep Creek is located within the British Mountains, which run perpendicular to the Firth River (Brooks and Lane 2011*). Vegetation in this area was primarily a function of elevation. At low elevations, it was dominated by sedges (*Carex* spp.) and stunted White Spruce (*Picea glauca* [Moench] Voss). Dense stands of White Spruce occurred on steep, mostly south-facing slopes. Low-growing vegetation, e.g., Eight-petalled Mountain Avens (*Dryas octopetala* [L.]) and Entire-leaved Mountain Avens (*D. integrifolia* Vahl) and lichens and scattered shrubs, such as willows (*Salix* spp.), Glandular Birch (*Betula glandulosa* Michaux), and alder (*Alnus* spp.) occurred at high elevations. Potential predators of nests and sandpipers in the study area included Gray Jay (*Perisoreus canadensis*), Common Raven (*Corvus corax*), Merlin (*Falco columbarius*), Northern Shrike (*Lanius excubitor*), and Arctic Ground Squirrel (*Citellus parryi*).

Methods

Nest location

In 2010, we searched for nests from 3 to 28 June. Nests were found opportunistically, while searching for songbird nests for a concurrent study (Turner 2013). Nests were monitored every 2–7 days until 2 July when the final egg hatched. Nests were checked, if there were no predators detected in the area, by flushing the adult bird from the nest. In 2011, the Upland Sandpiper was a focal species for our study. We searched for nests from 1 to 25 June in three ways: incidentally, while walking through potential home ranges; by dragging a 5-m rope, weighted down with tin cans, between two researchers; or with two or more researchers walking 2–3 m apart. Although we concentrated search efforts in open areas, we also searched areas typically not used as nesting sites by Upland Sandpipers, such as stands of stunted White Spruce on the flat, shallow slopes, and heavily forested areas. At discovery, we chose one egg from each nest and used the float stages described by Liebezeit *et al.* (2007), assuming a 21-day incubation period, to estimate hatch date (Houston *et al.* 2011). We monitored nests every 3–4 days during incubation and every 2 days after the estimated hatch date until eggs showed signs of hatching (starring or pipping), after which we checked nests daily until hatch. The last egg hatched on 10 July 2011. In both years, nest locations were recorded using a Garmin GPSMAP 60CSx global positioning system unit (Garmin International Inc., Olathe, Kansas, USA) and marked with naturally occurring objects placed within 10 m of nests to facilitate monitoring.

Nest success

We considered a nest to be successful if one or more eggs was alive or had hatched (judged by observation of adults with chicks or clean eggshell remnants in the nest) by the last visit. We considered nests abandoned when no adults were present in the area, or eggs were cold on three successive visits. We examined nests with missing eggs for evidence of predation (tracks or broken eggshells). We estimated daily survival of nests using the Mayfield estimate, assuming the nest was lost at the midpoint between the last visit when it was active and the first visit showing it had failed (Mayfield 1975; Johnson 1979). We compared tree density, distance to nearest tree, and vertical cover of successful and failed nests using two sample t-tests. We used the delta method (Powell 2007) for calculating the variance in period survival rate. We did not use logistic exposure methods or other models for our analysis of nest survival or habitat preferences because of the small number of nests in our sample. For all analyses, we set α at 0.05.

Habitat analysis

Most vegetation variables were assessed differently in 2010 and 2011 because of logistical constraints, but assessments were made within two weeks of hatching or nest failure in both years. In 2010, we measured vegetation characteristics at 10 nests and 10 random points in the park. In 2011, we also measured vegetation characteristics in 16 sampling plots within 50-m radius of the nest ("home range"), as well as 16 "nest" and 23 "park" sites. We did not document space use or movement, but selected a 50-m radius to include the presumed home range (Houston *et al.* 2011). Although Upland Sandpipers are known to breed in loose colonies and exhibit little territoriality, other populations have nests more than 300 m apart (Casey *et al.* 2011, Houston *et al.* 2011). To select sampling sites within the presumed home range, a random direction and distance up to 50 m from the nest were selected, excluding sites in water. To select park sites, we randomly chose coordinates in the study area using ArcGIS (ESRI, Redlands, California, USA) and located sites in the field using a GPS unit. Randomly chosen sites were excluded if they were in water, had a high tree density (> 80 trees with a diameter at breast height > 2.5 cm in an 11.3-m radius), or were more than 150 m above the treeline in dry, sparsely vegetated areas. No nests were found in these environments in either year.

In both years, we measured variables at two scales: microhabitat (1-m-radius plots) and mesohabitat (11.3-m-radius plots). In 2010, we measured height of the tallest vegetation in each cardinal direction within 5 cm of the point (using a ruler) and the elevation of the point (using a GPS unit and comparing with topographic maps for accuracy) at the microhabitat scale. We also visually estimated the proportion of the nest visible from 1 m above and the percentage cover of each species and other elements (water and bare ground) in the

microhabitat. Rare and short (< 1 cm) herbaceous species were ignored. At the mesohabitat scale, we paced the distance to the nearest tree (even if it was beyond the plot boundaries) or shrub greater than 1 m in height and recorded the plant species. The number of trees and shrubs over 1 m tall within the 11.3-m-radius plot was recorded, as well as the percentage cover of shrubs less than 1 m tall. The area of the habitat patch containing a nest or park site that did not contain trees was delineated by walking the inner perimeter of the surrounding trees using the track function on the GPS unit.

In 2011 at the microhabitat scale, we measured vegetation height near the nest cup and the elevation as in 2010. In addition, we visually estimated percentage vegetation cover, identifying each species (including dead sedges and grass), bare ground, water, litter, and lichens. The slope within the microhabitat was categorized as ≤ 5° or > 5°. Visibility from above was estimated by placing a 13-cm-diameter disc (the approximate diameter of most nests in our study) in the nest cup or at the centre of the home range or park microhabitat sites and estimating the proportion that was visible. The disc was brown and speckled black to resemble egg colouration. We recorded whether the site was on a hummock or flat ground. We also recorded the height of the tallest vegetation within the microhabitat radius (to the nearest mm), the species, whether it was dead or alive, and its direction and distance from the nest.

At the mesohabitat scale, we recorded the number and species of living and dead trees over 1 m tall, the number and species of shrubs over or equal to 1 m tall, and the percentage cover of shrubs less than 1 m. Trees less than 30 cm in height with a single stem were designated as seedlings and counted. The distance to the nearest tree or shrub over 1 m (even if outside the plot boundaries) in each cardinal direction (using an estimated 10° swath) was paced and the species was recorded, as well as the overall nearest tree and its direction. Percentage cover of the herbaceous layer, rock and bare ground, lichens, and water were visually estimated. Slope within the mesohabitat was visually estimated in the same categories as above.

Statistical analysis

All data were tested for normality and homogeneity of variances using Statistica v. 7.0 (StatSoft Inc., Tulsa, Oklahoma, USA). Data were transformed to meet the assumptions of parametric testing if necessary. If assumptions of normality were not met after transformation, we used non-parametric tests. We used ANOVA to determine whether vegetation height around the nest varied as a function of direction. We then calculated the average vegetation height adjacent to the nest for further analyses. Data for nest and park plots from 2010 at both microhabitat and mesohabitat scales were compared using t-tests.

Data for nest, home range, and park plots from 2011 at both microhabitat and mesohabitat scales were compared using ANOVA (for continuous data); equality of medians was compared using χ^2 and Kruskal Wallis tests (for nonparametric data) and χ^2 tests (for categorical data). Variables that were significantly correlated were removed from analysis. For example, height of tallest vegetation adjacent to the nest was correlated with the tallest vegetation within the microhabitat; thus, only the latter was retained for analysis. Before analysis, at the mesohabitat scale, we combined variables related to the number and percentage cover of shrubs and trees (e.g., numbers of trees over and under 1 m were combined). As results were similar for the combined and individual variables, we report results for combined variables only.

To assess differences in the composition of herbaceous plants at the microhabitat scale in both years, we used PERMANOVA, a permutational distribution-free method for assessing similarities in communities (Anderson 2005) and non-metric multidimensional scaling (MDS) plots with fourth-root transformed data using the Bray–Curtis similarity index. As vegetation cover was assessed differently in 2010 and 2011, this analysis was conducted separately by year. We excluded plant species that were present at fewer than three sites, as rare species have little effect on the Bray–Curtis distance, but increase stress. Stress represents distortion in MDS plots; a value under 0.2 is considered a good visualization of the data (Clarke and Warwick 2001; Clarke and Gorley 2006). We also combined similar species, such as Louseworts (*Pedicularis* spp.), to reduce the number of variables. We identified 15 species in 2010 and 39 species or genera in 2011. PERMANOVA requires a balanced design, so we randomly selected 16 of the park sites for comparison in 2011.

We first assessed the similarity of the dispersion between the nest, home range, and park sites using PERMDISP (Anderson 2005). Despite a significant difference in the dispersion between the groups for both 2010 and 2011 (see Results), we elected to complete the PERMANOVA analysis to explore the data. For both PERMDISP and PERMANOVA, we used 4999 permutations.

To represent relations among nest, park, and home range sites graphically, we used PRIMER v. 6.13 (PRIMER-E Ltd., Plymouth, UK) to create MDS plots. The axes of these plots do not relate to the original variables, but the proximity of points within the plots gives a relative measure of similarity (e.g., closer points are more similar, Proctor *et al.* 2012). A hierarchical cluster analysis using group averages created a cluster overlay on the plot. Resemblance levels of 20, 40, 60, and 80% were used with a slackness value of 75%.

We used t-tests to compare successful and failed nests (combining years to increase power) in terms of three habitat characteristics (vertical visibility, distance

to the nearest tree and number of trees in the mesohabitat).

Results

Microhabitat

Vegetation height adjacent to nests varied as a function of direction, with vegetation significantly lower east of the nests than in other directions ($F_{3, 73}$ = 3.13, P = 0.03); mean height of vegetation (± standard error): north, 13.2 ± 1.5 cm; east, 10.6 ± 1.6 cm; south, 13.4 ± 1.2 cm; west, 15.4 ± 1.5 cm. In 2010, neither average tallest vegetation adjacent to nests nor vertical visibility differed between nest and park sites (Table 1). Using PERMANOVA, we found a marginally significant difference in vegetation composition between nest and park sites ($F_{1,19}$ = 2.05, P = 0.08), and a significant difference in average within-group dissimilarities ($F_{1,19}$ = 8.64, P = 0.01). Vegetation cover around nest sites had greater similarity (61.6%) than at park sites (45.7%). Based on the MDS plot, stress was 0.16 and similarities between the majority of the points were over 40%.

Among the nests found in 2011, vertical visibility differed significantly between site types, with nest sites less visible than home range or park sites (Table 2). No other continuous microhabitat variables differed significantly between the three site types. Over half of all nests were on a gradual slope, but this proportion was not significantly different than that of home range and random park sites (Table 2). Nests were, on average, at an elevation of 254 m (similar to the value from 2010, Table 1), a value that also did not differ significantly from home range or random sites (Table 2). Nest and home range sites were significantly more likely to be in hummocky habitats (> 80%) than random park sites (47.8%).

In 2011, as in 2010, we found no significant differences in composition of the plant communities at nest, home range and park sites (PERMANOVA, N = 48, $F_{2,47}$ = 1.25, P = 0.24). The MDS plot shows that similarity of plant composition between points is over 40% and nest sites are concentrated toward the upper centre of the MDS plot (Figure 1). There were significant differences in within-group vegetation composition for all three site types (PERMDISP, $F_{2,47}$ = 6.45, P = 0.002), with nest sites more similar than both park and home range sites, which were not different (Table 3).

Mesohabitat

Upland Sandpipers nested in Arctic and alpine tundra and wet sedge meadows, although they were restricted to drier locations in the latter. Nests occurred in both small and large clearings within the scattered stunted White Spruce. Most random park sites and nearly all home range locations were on gradual slopes, reflecting the hilly nature of the study area. Water in the park, home range and nest mesohabitat plots was relatively rare (≤ 25%; Table 2). The openings used for nesting were small (< 0.1 ha), but these did not vary significantly in size from openings in the random park sites (Table 1).

Vegetation characteristics at this scale were similar between nest and park sites in 2010 (Table 1). In 2011, park sites had significantly more trees and less herbaceous cover than either home range or nest sites, which did not differ from each other (Figure 2, Table 2). None of the remaining variables differed across site types.

We found no significant differences between successful and unsuccessful nests in vertical visibility (t_{23} = 1.18, P = 0.25), distance to the nearest tree (t_{23} = 0.63, P = 0.53), or number of trees in the mesohabitat (t_{23} = -0.92, P = 0.37). Inter-nest distances were 288 ± 45 m in 2010 and 234 ± 42 m in 2011.

Nest survival

In 2010, we found 10 nests, eight with four eggs, one with three eggs and one with two chicks. In 2011, we found 16 nests, 14 with four eggs, one with three eggs and one after the chicks had hatched and left the nest. In 2010, eight nests hatched successfully, one nest contained whole broken shells on the last visit, and one nest was abandoned, while in 2011, nine were successful,

TABLE 1. Comparison of habitat characteristics at micro and meso scales between Upland Sandpiper (*Bartramia longicauda*) nest sites and random "park" sites at Sheep Creek, Ivvavik National Park, 2010.

Habitat characteristic	Mean (± SE) or median (range)		P
	Nest (n = 10)	Park (n = 10)	
Microhabitat			
Elevation, m*	249.5 (239–293)	n/a	—
Height of adjacent vegetation, cm	11.3 ± 1.4	10.7 ± 1.7	0.83
Vertical visibility, %*	91.5 (60.0–97.0)	82.5 (0.0–100.0)	0.85
Mesohabitat			
Area of clearing, m²	492.8 ± 261.3	474.6 ± 405.1	0.97
Distance to nearest tree, m	3.4 ± 0.9	4.5 ± 1.0	0.41
Shrub cover, %	14.5 ± 2.8	12.4 ± 2.5	0.59
Number of trees over 1 m tall†	17.1 ± 8.6	24.3 ± 5.0	0.48

Note: n/a = not applicable, SE = standard error.

*Results are presented as median (range) as the data do not conform to assumptions of normality.

†Log_{10} transformation used for analysis; means presented as untransformed data.

TABLE 2. Comparison of habitat characteristics at micro and meso scales among Upland Sandpiper (*Bartramia longicauda*) nests, random home range sites and random park sites at Sheep Creek, Ivvavik National Park, 2011.

Habitat characteristic	Mean (± SE), median (range), or proportion (%)			
	Nest (n = 16)	Home range (n = 16)	Park (n = 23)	P
Microhabitat				
Elevation, m*	254 (240–356)	260 (247–450)	254 (238–359)	0.30
Tallest vegetation, cm†	30.4 ± 1.8	44.6 ± 6.3	54.7 ± 13.1	0.11
Distance to tallest vegetation, cm	62.7 ± 7.6	74.3 ± 5.9	79.2 ± 5.3	0.17
Vertical visibility, %*	91.5 (70.0–98.0)	99.0 (85.0–100.0)	99.0 (82.0–100.0)	0.0004‡
Proportion (%) on hummock	14/16 (87.5)	13/16 (81.3)	11/23 (47.8)	0.01‡
Proportion (%) on gradual slope	11/16 (68.8)	7/16 (43.8)	11/23 (47.8)	0.30
Mesohabitat				
Herbaceous cover, %	70.7 ± 3.0	61.5 ± 5.2	56.2 ± 3.7	0.04‡
Lichen cover, %§	2.2 ± 0.7	1.6 ± 0.6	2.3 ± 0.7	0.62
Bare ground, %†	2.5 ± 0.56	6.0 ± 2.5	5.1 ± 1.6	0.81
Shrub cover, %	18.2 ± 2.9	23.7 ± 4.8	22.5 ± 2.9	0.55
Number of shrubs over 1 m*	0.0 (0.0–2.0)	0.0 (0.0–35.0)	0.0 (0.0–18.0)	0.20
Number of saplings*	0.0 (0.0–4.0)	0.0 (0.0–4.0)	0.0 (0.0–38.0)	0.18
Proportion (%) on gradual slope	11/16 (68.8)	7/16 (43.8)	17/23 (73.9)	0.14
Proportion (%) with water	3/16 (18.8)	4/16 (25.0)	2/23 (8.7)	0.37
Number of trees§	10.3 ± 3.0	9.4 ± 3.3	32.9 ± 5.9	0.004‡

Note: SE = standard error.
*Results are presented as median (range) as the data do not conform to assumptions of normality.
†Inverse transformation; means presented as untransformed data.
‡Significant differences between site types.

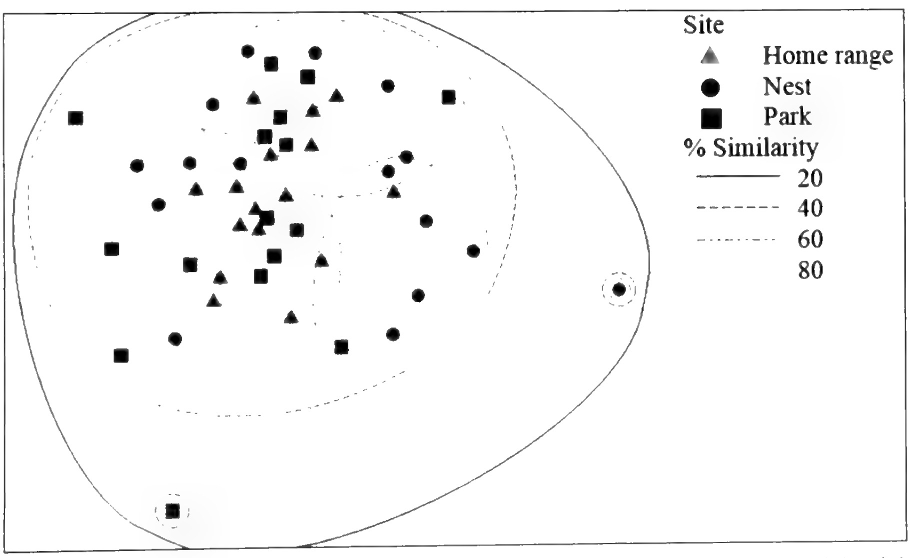

FIGURE 1. Non-metric multidimensional scaling plot of vegetation in the microhabitat at Upland Sandpiper (*Bartramia longicauda*) nests, random home range sites and random park sites at Sheep Creek, Ivvavik National Park, Yukon, Canada, 2011. Using the Bray–Curtis similarity index, the cluster overlay has resemblance levels of 20, 40, 60, and 80 % and a slackness of 75%. Close points indicate sites with more similar plant composition. Stress was 0.18.

TABLE 3. Comparison of within-group similarity of vegetation at Upland Sandpiper (*Bartramia longicauda*) nests, random home range sites and random park sites at Sheep Creek, Ivvavik National Park, 2011, using PERMDISP.

Site type	Bray–Curtis index (average within group similarity), %	Comparator	t	P
Nest	66.3	Home range	2.7	0.009
Home range	56.8	Park	4.0	0.001
Park	54.6	Nest	0.7	0.520

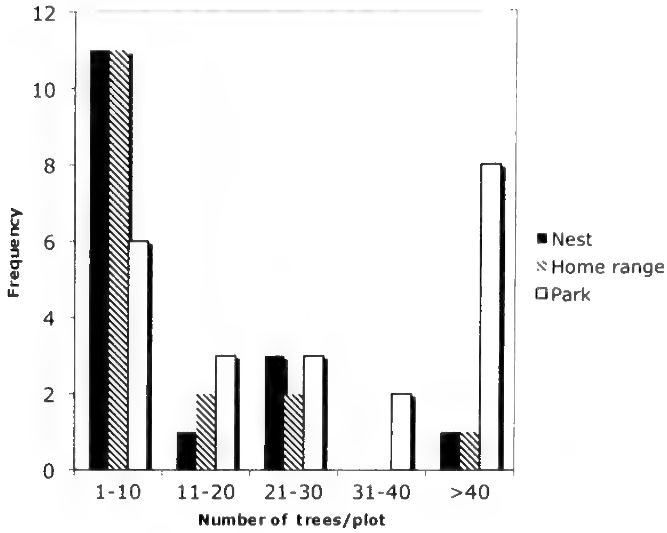

FIGURE 2. Frequency distribution of number of trees in the mesohabitat (11.3-m-radius plots) at Upland Sandpiper (*Bartramia longicauda*) nest and home range sites and random park sites at Sheep Creek, Ivvavik National Park, Yukon, Canada, 2011.

seven were unsuccessful, and the fate of two nests remained uncertain. Mayfield estimates of daily nest survival were 0.989 ± 0.007 (n = 10) in 2010 and 0.976 ± 0.010 (n = 14, excluding the two uncertain nests) in 2011 for period survival rates of 0.851 ± 0.135 and 0.558 ± 0.118, respectively, assuming a 21-day incubation period.

Discussion

Of the many habitat variables we compared in this study, only a few affected the choice of nest site by Upland Sandpipers. As predicted, Upland Sandpipers nested in home ranges with fewer trees and greater herbaceous cover than found generally in this treeline region, although trees in the park were also relatively sparse (32.4 trees/ha). Upland Sandpipers placed their nests at sites with more vertical cover than available in their putative home ranges. The composition of low-lying species of Arctic plants within the nest sites was less variable than in the home range, suggesting that a site with a relatively homogeneous plant community is sought. Most nests were placed in areas dominated by sedges, with a mixture of Mountain Avens, Lapland Rosebay (*Rhododendron lapponcium* [L] Wahlenberg), mosses, and willows. None of the variables we studied predicted nest success of the Upland Sandpiper, although our sample size of nests was small.

Vegetation east of the nests was 2–5 cm shorter than in other directions. Upland Sandpipers probably entered the nest cup consistently from the east, facing into the predominant northwest wind, which would result in some trampling of vegetation. Orienting into the wind both reduces ruffling of the feathers (Gochfeld 1978) and gives incubating bird greater cover from wind, thus reducing conductive cooling.

Use of grasslands and other treeless habitats is a characteristic of the Upland Sandpiper in the southern and central part of its range (Kirsch and Higgins 1976; Ailes 1980; Bowen and Kruse 1993; Dechant *et al.* 2003*). In North Dakota, occupancy of mixed-prairie grassland by Upland Sandpipers is negatively correlated with the proportion of woodland. Therefore, Upland Sandpipers are designated a woodland sensitive species (Grant *et al.* 2004). Trees may provide perches for avian predators, as well as for their prey, increasing the potential for higher abundance and activity of predators associated with woody vegetation. Simultaneously, trees reduce visibility and diminish the ability of incubating adult Upland Sandpipers to sense these predators (Johnson and Temple 1990; Winter *et al.* 2000; Coppedge *et al.* 2001; Chapman *et al.* 2004; Grant *et al.* 2004; Graves *et al.* 2010). Although Upland Sandpipers avoided trees at the scale of their nests and home ranges in the Yukon, they did use trees in the landscape for perching and vocalizing while we were in the area of their nests. Shrub cover in northern Yukon may not have influenced Upland Sandpipers, as the majority of the shrubs in this habitat were short (< 20 cm), not much taller than the herbaceous layer, and scattered in distribution. In addition, during the nesting season, the shrubs had limited to no foliage, thus reducing the effect on visibility.

Upland Sandpipers selected nesting sites with greater vertical cover or less visibility than random sites within the home range. Vertical or overhead cover, mostly by grasses and sedges in our study, can increase nest success by reducing visibility, especially for avian predators, and reduce egg loss from predation (Dwernychuk and Boag 1972; Martin 1993; DeLong *et al.* 1995; Stokes and Boersma 1998; Dion *et al.* 2000). The ben-

eficial effect of overhead cover is especially important during incubation recesses when the movement of adults can make the nests more susceptible to avian predators (Smith *et al.* 2012). While incubating, Upland Sandpipers have a highly cryptic plumage, and the additional grasses and other plants that protruded around the nest cup probably decreased their conspicuousness even more. Overhead cover can also help to retain warmth around the nests (With and Webb 1993). As mean temperatures ranged from −4.2° to 26.9° C during incubation in Ivvavik National Park (Government of Canada 2014), features that reduce temperature stress on the incubating Upland Sandpipers may improve reproductive success.

Variation in plant species cover in the microhabitat around nests was lower than at random sites in the home range or park, although there was no significant difference in the amount of species cover. The reduced variation at nests suggests that Upland Sandpipers are avoiding sites at the extremes. For example, the maximum amount of bare ground at nesting sites was 9.0%, whereas at home ranges, it was 91.0% and at park sites 28.5%. Upland Sandpipers did not use sites that were wet, where *Equisetum* spp. were common, or dry, rocky sites, where *Dryas* spp. were common. Bare ground could occur at either dry sites where rocks and exposed ground were common or wet sites where the water had receded. In the future, vegetation should be categorized by habitat type (i.e., wet, dry, etc.) or structure, rather than by individual species, as it is unlikely that Upland Sandpipers can distinguish between plant species of similar height and shape.

Nest success (56–85%) in this northern breeding population was at the high end of the range reported from other more southerly locations (see review in Garvey *et al.* 2013). This observation, albeit based on a small sample size, is consistent with predictions regarding a latitudinal effect on predation risk (McKinnon *et al.* 2010). Contrary to our predictions, nest success was not influenced by either distance to trees or number of trees at the mesohabitat scale, nor vertical cover. This may have been due to the small sample size of failed nests or because of a diverse predator community. When there is a diverse predator community that uses various cues and searching methods to find nests, it can result in no adaptive signal of habitat selection (Braden 1999, Dion *et al.* 2000). Further exploration of the relation between predator abundance and an encroaching treeline is needed in this northern location. In the prairies, Clay-colored (*Spizella pallida*) and Vesper Sparrows (*Pooecetes gramineus*) have greater nest survival near forest edges, as their main predator (the Thirteen-lined Ground Squirrel, *Ictidomys tridecemlineatus*) is primarily found in grassland interiors (Grant *et al.* 2006). By contrast, in predominantly forested areas, many species experience lower reproductive success near edges (Burke and Nol 2000). The nesting success of Upland Sandpipers in the Canadian prairies appears to be predominantly influenced by nest age and not by landscape features (Garvey *et al.* 2013), a result that is similar to our findings.

We have provided the first detailed description of the habitat of nesting Upland Sandpipers at the northern edge of their range. As in the prairie regions, Upland Sandpipers in the northern Yukon breed in home ranges with less tree cover and greater herbaceous cover than what is randomly found. Within Ivvavik National Park, Upland Sandpipers are restricted to inland, sparsely treed regions (Brown *et al.* 2007). In addition, within the park, Upland Sandpipers nest in flat valleys and along shallow slopes, as the mountains are too rocky for this grassland species and the steep, south-facing slopes have dense spruce cover. As early as the middle of the last century, Buss (1951) suggested the potential for habitat loss for Upland Sandpipers in the southern Yukon because of encroachment of vegetation into the clearings used for breeding. Given the already small openings (< 0.1 ha) in the sparsely forested landscape where Upland Sandpipers nest, habitat loss as a result of northward shrub and tree encroachment with climate warming is a real threat to this population's persistence.

Acknowledgements

We are extremely grateful for funding provided by Parks Canada, the Wildlife Management Advisory Council (North Slope), the Natural Sciences and Engineering Research Council and its Undergraduate Student Research Award program, and the Northern Scientific Training Program. We are especially grateful to Kayla Arey, whose plant identification expertise was invaluable. We thank the Parks Canada's Western Arctic Field Unit employees and volunteers for assistance with logistics and fieldwork. We also thank Brett Sandercock for detailed comments on an earlier version of this manuscript.

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Received 13 June 2013
Accepted 30 August 2013

Cory's Bittern, *Ixobrychus "neoxenus" exilis*: Morph, Mutant, or Mixed Bag?

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Smith, Paul. 2014. Cory's Bittern, *Ixobrychus "neoxenus" exilis*: morph, mutant, or mixed bag? Canadian Field-Naturalist 128(4): 350–357.

Cory's Bittern (*Ixobrychus "neoxenus" exilis*) is an enigmatic form, usually referred to as a rare dark colour phase or morph of Least Bittern (*Ixobrychus exilis* [Gmelin, 1789]). A review of the literature indicates that birds identified as Cory's Bittern show considerable plumage variation and commonly exhibit multiple plumage anomalies. Temporal and spatial clumping of records shows that they are of irregular occurrence; thus, they do not meet the criteria for recognition as a colour morph. Cory's Bittern should thus be viewed as a colloquial name that refers to any one of a number of abnormally dark-plumaged, genetically undefined and phenotypically heterogeneous Least Bitterns.

Key Words: Cory's Bittern; *Ixobrychus neoxenus*; *Ardetta neoxena*; Least Bittern; *Ixobrychus exilis*; leucism; melanism; Ontario; Florida

Introduction

Since its description as *Ardetta neoxena* (Cory 1886a, b), Cory's Bittern has captured the attention of ornithologists on account of its extreme rarity, striking plumage and disjunct distribution. Despite the confident assertion that the form is "without doubt perfectly distinct from any other known species" (Cory 1886a), doubts over its specific identity were soon expressed. After examining a number of specimens and publishing a series of papers (Scott 1889, 1891), Scott (1892a) stated, "I feel impelled to record the strong impression that I entertain, that it will ultimately be found to be a color phase of *Botaurus exilis*." Sharpe (1894) expressed the controversial opinion that "*Ardetta neoxena* of Cory seems to be founded on very old individuals of *A. exilis*, in which the rufous tips to the quills and the light stripes on the back have disappeared with age or wear," although on examination of a specimen, he later afforded it full species status (Sharpe 1898). Bangs (1915), on the other hand, referred to Cory's Bittern as a "case of nothing more or less than erythrism."

Bent (1926) concurred with the impression that Cory's Bittern is conspecific with Least Bittern (*Ixobrychus exilis*), but warned, "It should not be called a color phase of a dichromatic species, as it occurs too rarely and irregularly." Hellmayr and Conover (1948) indicated that "*neoxenus*" was synonymous with *exilis* and followed Bent in describing it as a "melano-erythristic mutation."

In a thorough review of the state of Cory's Bittern knowledge, Pittaway and Burke (1996) speculated that "Cory's Least Bitterns seen today probably result from a rare recessive allele in the population of typical birds" and that "The lack of intermediate morphs between typical and Cory's Least Bittern suggests a single gene having two alleles for colour: dominant (typical) and recessive (Cory's)." The authors lamented the lack of available genetic material and highlighted the speculative nature of this hypothesis. This theory has subsequently been adopted in the modern literature (Hancock and Kushlan 1984; Gibbs *et al.* 1992; Sibley 2000), perhaps stemming in part from a widespread but incorrect understanding of the term "morph."

Polymorphism is correctly defined as "the coexistence in one interbreeding population of two or more distinct and genetically determined forms, the least abundant of which is present in numbers too great to be due solely to recurrent mutation" (Ford 1945). Polymorphism can occur in two forms: transient (where an advantageous gene spreads through the population) and balanced (where it is maintained at a fixed level by a balance of selective agencies). The definition "excludes continuous variation… and the appearance of heterozygous mutants subject to elimination by selection" (Ford 1955). As this definition excludes both plumage abnormalities (as suggested by Bent 1926) and the segregation of rare recessives (suggested by Pittaway and Burke 1996), the status of Cory's Bittern requires clarification.

This paper is a critical review of the published data that aims to re-examine the status of "*neoxenus*," with the hope that a pilot genetic study will one day be conducted to confirm or dismiss the hypotheses proposed.

Spatial Distribution

Cory's Bittern is known from very few documented records, most of which are from eastern North America before 1900 (Palmer 1976; Pittaway and Burke 1996; Sibley 2011) (Figure 1). Despite the range of the Least Bittern in the Americas — stretching from southern Canada to northern Argentina (Hancock and Kushlan

1984) — the 38 documented North American records are of the migratory subspecies *exilis* and are concentrated around the Great Lakes and Florida, with 22 records from Ontario; 7 from Florida; 2 each from Michigan, Ohio, and Illinois; and 1 each from Massachusetts, New York, and Wisconsin (Brewster 1902; Kumlien *et al.* 1948; Palmer 1976; Pittaway and Burke 1996; Sibley 2011). Additional undocumented sight records are listed by Pittaway and Burke (1996) and Sibley (2011) but, with the exception of a pair of recent reports by the same observer (D. Arbour, of Red Slough, Oklahoma – 15 August 2001 and 14 May 2012), they do not expand the known distribution.

All three South American records are of the resident subspecies *erythromelas* and are confined to a comparatively small area of southern Brazil (São Paulo State and Mato Grosso do Sul [Teixeira and Alvarenga 1985; Sibley 2011]) and adjacent Paraguay (Asunción [Clay *et al.* in press]). Though only one of the individuals was collected (Teixeira and Alvarenga 1985), the other two were documented by video (Sibley 2011) and photograph (Clay *et al.* in press) respectively. The South American subspecies are non-migratory, but undertake local movements in response to water conditions (Martínez-Vilalta and Motis 1992).

Temporal Distribution

All Ontario specimens of Cory's Bittern were taken in the breeding season between May and September (Cross 1892; Brown and Brewster 1893; Fleming 1902; Pittaway and Burke 1996; Sibley 2011), and 21 of the 22 specimens from Ontario were taken in a 10-year period between 1890 and 1900, with a single additional specimen taken in 1913. Pittaway and Burke (1996) list undocumented sight records from Ontario in "about 1921," 1923, 1927, 1928, 1932, 1939, 1941, 1950, "in the 1950s," 1973, and 1981. Cory's Bittern has thus not been documented in the "stronghold" of its range since 1913 and not reported there since 1981. Images of the specimens held in the Royal Ontario Museum can be consulted online at www.jeaniron.ca/2011/corys.htm.

Six of the first seven specimens of Cory's Bittern were taken in Florida, although the description of the type specimen taken in Florida in 1885 lacks a precise date (Cory 1886a): five specimens were taken between 9 July 1889 and 15 August 1891 (Scott 1889; Cory 1891; Chapman 1896). Although Scott (1892b) describes it as occurring "regularly though probably in small numbers at Lake Flirt and Lake Okeechobee," the next report from Florida was not until Bent and Copeland (1927) saw a bird on 7 April 1925. There are no further Florida reports until an undocumented sight record by J. Brunner in April 2003 (Sibley 2011). There have been no documented records of Cory's Bittern in Florida, the second core area of the range, for almost a century. All records correspond approximately to the breeding season.

The first Ohio specimen of Cory's Bittern was collected on 25 May 1907 in a "large colony of Least Bitterns" (Ruthven 1907), and the second, possibly a migrant bird, was photographed after flying into a building at Youngstown on 3 October 1949 (Pittaway and Burke 1996). In Illinois, Carpenter (1948) took a specimen on 1 June 1909 and another was collected by Eifrig (1915) on 23 May 1914. Cherrie (1896) reported the only specimen from Wisconsin, a male in full plumage on 22 May 1893, while Watkins (1895) reported a "fine male" from Michigan on 8 August 1894, which was followed by another Michigan male taken on 14 May 1904 (Taverner 1905). Brewster (1902) documents the only Massachusetts record, collected in a "yard" on 18 May 1901. Allen (1913) includes a photograph of a female taken at the Ithaca marshes, New York on 17 May 1913, although Bull (1985) was later unable to trace this specimen. Two modern sight records from Oklahoma — 15 August 2001 and 14 May 2012 — were also during the breeding season, but far removed from the traditionally understood "core range."

South American records account for almost half of the seven worldwide records since the 1950s (and all of the documented records), but none of the records prior to that date (Teixeira and Alvarenga 1985; Sibley 2011; Clay *et al.* in press). All South American records have been taken in the austral autumn during April and May. Consequently, all dated reports of Cory's Bittern are between April and October, with no reports from anywhere in the entire range between November and March. Wintering grounds, migration routes, and whether these differ from those of "normal" birds are all unknown.

Variation

Cory (1886a) described his *Ardetta neoxena* as "Top of the head, back, and tail dark greenish black, showing a green gloss when held in the light. Sides of the head and throat rufous chestnut, the feathers on the back of the neck showing greenish black tips. Breast and underparts nearly uniform rufous chestnut, shading into dull black on the sides; wing-coverts dark rufous chestnut; under wing-coverts paler chestnut. All the remiges entirely slaty plumbeous. Under tail-coverts uniform dull black." In addition he noted the presence of two white flank feathers, which he attributed to "albinism." Subsequent published descriptions of specimens ascribed to *neoxena*, however, show considerable divergence from this type description; some examples are summarized below.

Chapman (1896) noted great variation in the plumage of Cory's Bittern: "only three of my ten specimens of *neoxena* are alike." In comparing it to typical *exilis*, he added, "there is no regularity in the substitution of colors; hence these birds differ not alone in color, but also in pattern of coloration." Significantly, he added, "Nor do the known cases of dichromatism among Herons give us any ground for asserting that

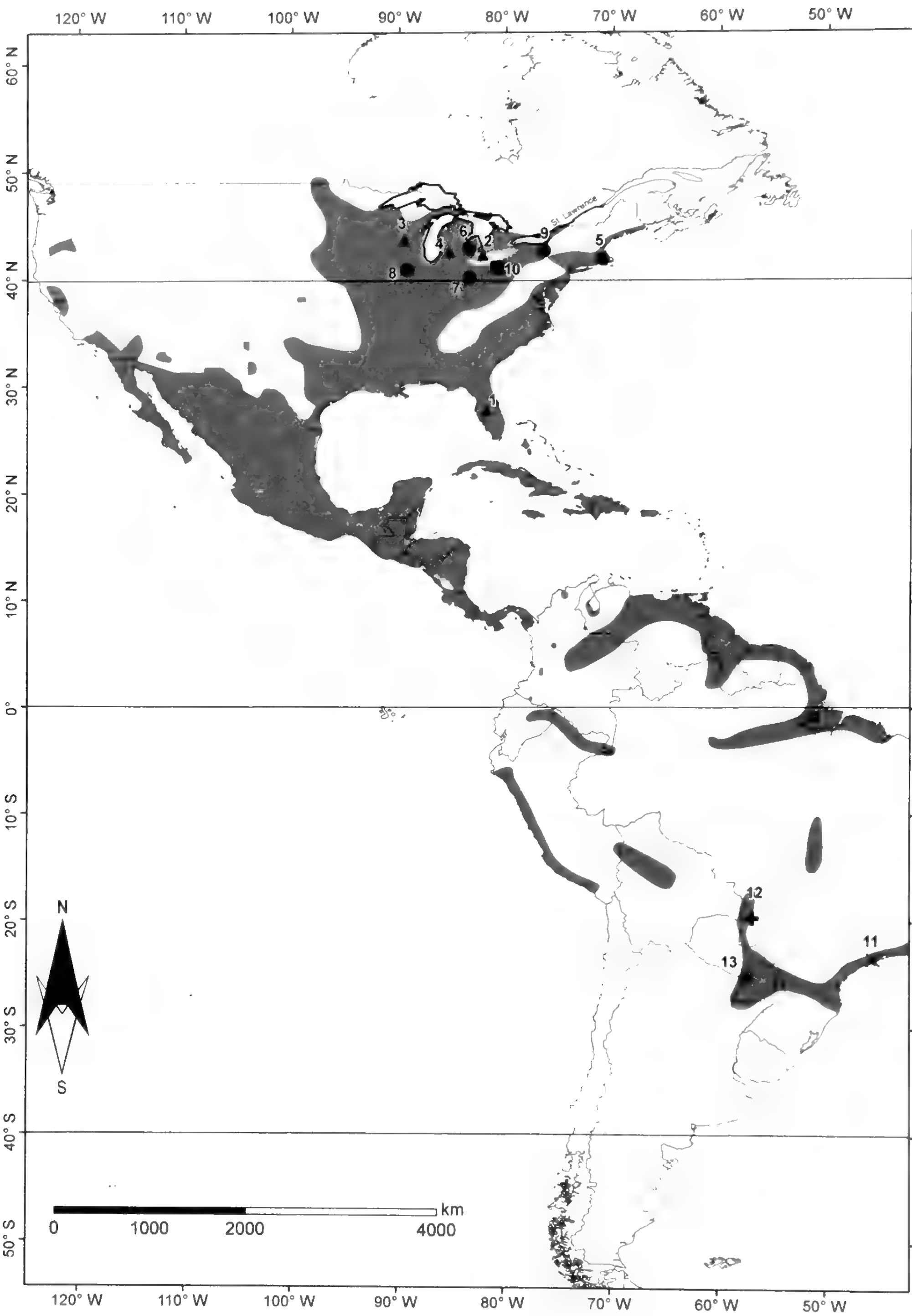

FIGURE 1. Distribution of the Least Bittern, *Ixobrychus exilis* (grey shading; BirdLife International and NatureServe 2013), and reports of Cory's Bittern (*I. "neoxenus" exilis*) in North and South America documented in 1880–1900 (triangles), 1900–1920 (circles), 1940–1960 (squares) 1960–1970 (cross), and 2010–2013 (plus signs). 1. Lake Okeechobee area, Florida, USA (Cory 1886a; Scott 1892a); 2. Toronto area, Ontario, Canada (Brown and Brewster 1893); 3. Lake Koshkonong, Wisconsin, USA (Cherrie 1896); 4. Jackson County, Michigan, USA (Watkins 1895); 5. Scituate, Plymouth County, Massachusetts, USA (Brewster 1902); 6. St Clair Flats, Michigan, USA (Taverner 1905); 7. Toledo, Ohio, USA (Ruthven 1907); 8. Rob Roy Marsh, Aurora, Illinois (Carpenter 1948) and Fox River, 40 miles northwest of Chicago, Illinois, USA (Eifrig 1915); 9. Ithaca Marshes, New York, USA (Allen 1913); 10. Youngstown, Ohio, USA (Pittaway and Burke 1996); 11. São Paulo, Brazil (Teixeira and Alvarenga 1985); 12. Pantanal, Mato Grosso do Sul, Brazil (Sibley 2011); 13. Asunción, Paraguay (Clay et al. in press).

neoxena is a dichromatic phase of *exilis*." However, while admitting that he could not "explain this unusual degree of variation," he opted instead to ignore it and consider Cory's Bittern a distinct but presumably highly variable species. Although seven of his ten specimens showed "melanistic or albinistic markings or both combined," Chapman (1896) did not consider the possibility that the form represented a heterogeneous range of phenotypic variations caused by diverse plumage abnormalities.

A male specimen from Florida (no. 44 806) is described as "completely melanistic" (Chapman 1896), while Carpenter (1948) reported a Cory's Bittern from Illinois that was "extremely albinistic yet decidedly melanistic," in which the pale areas of the plumage were entirely white, several irregular black patches were present, and there were only scattered chestnut feathers on the underparts. Allen's (1913) specimen from New York, however, showed no "albinistic tendencies." A sight record reported by Alex Lucas on 2 August 1939 along the Otonabee River at Rice Lake, Peterborough County, Ontario, was described as "chocolate-colored all over" (Pittaway and Burke 1996).

The second known specimen of Cory's Bittern reported by Scott (1891) from Florida (no. 3237) was described as "deep greenish-black" on the "entire upper surface," with this colour "also the general tone of the belly, sides, and flanks, though a few whitish and some chestnut feathers are mixed" and "bright chestnut" only on the "lower surface of the neck and throat." Furthermore, the greater, median, and mid lesser coverts are "dark like the back at the bases but shade into deep chestnut terminally."

A male specimen (no. 11 449, collection of W. E. D. Scott), also reported by Scott (1892a), is also dark greenish-black "both above and beneath," differing yet again in that the "feathers of the lower neck alone having traces (edgings) of dark chestnut, their centres being of the greenish black tone prevailing throughout the bird." In the same paper (no. 11 451) is said to be "very like Mr. Cory's original bird save that there are traces on the sides of the back of lines, much obscured, but of a general brownish tint, thus approaching *Botaurus exilis*." Cherrie's (1896) Wisconsin specimen, a male in full breeding plumage, "agrees minutely above (with the type specimen)" but below "the throat and neck are just a trifle paler chestnut, and there is just a little more white on the abdomen." Brewster's (1902) Massachusetts specimen had the "flanks, abdomen and under-tail coverts, slaty brown tinged with reddish."

In addition to other black markings on the head, the second specimen from Michigan reported by Taverner (1905) had a "triangular patch of black" below and behind the eye that reached from the bill before fading out on the ear coverts. Fleming's (1902) adult male (no. 14, collection of the Provincial Museum of Toronto) has chestnut sides of the head and the breast and abdomen black "slightly tinged with chestnut" but possesses "a clearly-marked black line running from the gape almost to the back of the head, on both sides,... [that] nearly divides the chestnut on the sides of the head."

Among the three modern South American records, similar variation is present. Teixeira and Alvarenga's (1985) bird did not show any greenish gloss on the black areas of the plumage and had entirely black secondaries. The specimen from Paraguay does show the greenish gloss on the black areas of the plumage, but possesses the typical yellowish bill colouration of "normal" *exilis*, not the "mostly blackish brown" associated with Cory's Bittern (Pittaway and Burke 1996), and has a black medial line down the centre of the foreneck (Clay *et al.* in press).

Fleming (1902) reports a young male (no. 15, collection of the Provincial Museum of Toronto) with "peculiar" feet so that "the green of the tarsus and toes is curiously mottled and blotched with reddish brown," leading to the speculation that "it may prove that the feet and legs of the nestlings are not colored as in the adult." However, the colour of the legs is not mentioned in the description of the type and in the subsequent literature is variably described as "blackish to brown" (Eifrig 1915), "dark(er) olive-green" (Sibley 2011), and brownish without yellow tinges (Teixeira and Alvarenga 1985), while the photograph in Clay *et al.* (in press) shows legs that resemble those of typically plumaged birds.

The morphometrics of Cory's Bittern have received scant attention. Chapman (1896) provided limited data for a small number of specimens that he examined, but elected not to discuss the results in his text. Presumably he was unable to detect any obvious diagnostic characteristics in his data.

Assortative Mating

In an attempt to explain the high rate of partial leucism in specimens of Cory's Bittern, Pittaway and Burke (1996) offered assortative mating resulting in inbreeding as a potential, if "unlikely" explanation. Thus, it may be inferred that the other highly variable plumage characteristics exhibited by the birds are to be treated as normal "morph" plumage. With no more likely explanation consistent with a morph hypothesis offered to explain the strong link with leucism, it seems relevant to address the evidence for assortative mating.

The tendency for Cory's Bittern to pair with other Cory's Bitterns was first reported by Scott (1891) recounting a letter received by him from Mr. J. F. Menge of Fort Meyers, Florida, regarding a nest discovered on 8 June 1890. Although the letter mentions four young birds in the nest, Mr. Menge did not provide a description of them and alludes to the parent birds, again without description. Never having seen these birds, Scott relies solely on this secondhand account. Fleming (1901) refers to a female on a nest, but again there is no description of her and no mention of her

mate. The assumption clearly made by the author is that Cory's Bittern is a valid species and, hence, the mate must be of the same species, an assumption supported by Ames (1901) who, describing the same bird and eggs, refers to it as *Ardetta neoxena*. Bent and Copeland (1927) recount another secondhand report from Mr. Oscar E. Baynard, who found a nest in Florida in 1927 and stated that "the young are always as black as Clapper Rails and that both adults are always dark-colored, evidence supporting the view that Cory's Least Bittern is a distinct species." The certainty expressed is at odds with the conclusions that may be reasonably drawn from an undocumented report of a single nest. Perhaps the only actual evidence of association in these birds is of a male and a female collected at Ashbridge's Bay, Toronto on 12 July 1900, although there is nothing to suggest that these birds were breeding or had even formed a pair beyond the collection date. In addition, a single pair of mated Cory's Bitterns would not be considered proof of assortative mating.

Although there is no real evidence that Cory's × Cory's pairs are the norm, there are also no published reports of mixed pairs as occurs commonly in other polymorphic herons (Hancock and Kushlan 1984). In fact the data available are too limited and unreliable to draw any conclusions at all.

Assortative mating as a consequence of mate choice based on morph appearance is extremely rare in birds and has been documented in the wild in very few avian taxa. In some polymorphic geese, for example, most birds select a mate with colour or pattern similar to that of the family in which they were raised (Cooke 1978; Abraham *et al.* 1983). However, even in these instances a considerable percentage of the pairs are mixed (15–18% in the Snow Goose, *Anser caerulescens*), rendering secondhand statements that Cory's Bittern always mates with like highly suspect. Kalmus and Maynard-Smith (1966) and Seiger (1967) go so far as to state that sexual imprinting leading to absolute assortative mating in a species with two morphs would be a speciating mechanism.

Early authors convinced of the species status of *neoxena* and the collectors who supplied them with these valuable birds may be forgiven for assuming or even promoting the idea of like with like pairs. Clearly, early collectors were aware of the financial benefits that species status brought, and Pittaway and Burke (1996) mention at least one well-known Ontario collector, George Pearce, who destroyed specimens of normal *exilis* to promote the idea of species status and even dyed normal birds to sell to collectors. Perhaps not coincidentally, the same collector is the author of a supposed sight record of breeding birds at Lake Erie in 1923 (Pittaway and Burke 1996).

Pittaway and Burke (1996) do not assume assortative mating (although the references they cite do) and refer to assortative mating of any kind as "unlikely." However, adopting the more likely scenario leaves us without an explanation as to why, if it is indeed a morph, Cory's Bittern shows such high levels of leucism and such random plumage variation overall.

Discussion

Although many specimens attributed to Cory's Bittern have shown only superficial similarity to the description of the type (Carpenter 1948), the extraordinary degree of plumage variation exhibited by specimens of Cory's Bittern seems to have been largely overlooked by modern authors.

Cory's Bittern specimens referred to as "partially albinistic" are more properly described as "partially leucistic" (van Grouw 2006). The enzyme tyrosinase, necessary for the chemical processes that produce melanins in vertebrates, is present in leucistic individuals but absent in albinistic ones; hence, partial albinism cannot exist (van Grouw 2006). Partial leucism is not an indicator of genetic health, as it results from an inherited disturbance disorder of pigment transfer during which deposition of melanin in the feather cells fails to occur (van Grouw 2006). According to Kettlewell (1973), "Melanic, melanistic and melanochroic forms refer to heterogeneous and genetically quite indeterminate groups." Furthermore multiple types of plumage aberrations in a single individual are often indicative of a genetic defect influencing several pigmentation systems (Buckley 1982; Davis and Blumin 2012). The irregular and varied plumage types seen in Cory's Bittern are thus explicable in the context of plumage aberrations resulting from genetic defects and are not consistent with the "distinct and genetically determined forms" required for recognition of polymorphism (Ford 1945, 1955). The variation observed is so great, in fact, that it is not even possible to attribute it to a single plumage aberration. Specimens ascribed to *neoxenus* seem to exhibit a random assortment of eumelanistic, leucistic, and phaeomelanistic aberrations, and potentially others, each of which may be influenced by any number of genes and pathways.

The localized spatial and temporal distributions of the birds led Pittaway and Burke (1996) to suggest that these represent places "where random processes allowed the Cory's morph to become temporarily established, because of chance colonization by a few individuals with the trait." However this begs the question: where did these colonizing individuals come from? The alternative and mutually exclusive explanation offered by the same authors is that Cory's is "an older form that is now at a selective disadvantage and has been replaced by the typical morph" (Pittaway and Burke 1996). However, this ignores the fact that the records clump temporally as well as spatially. In the context of a morph hypothesis, the first statement approximates transient polymorphism, but selective advantage is not consistent with an association with plumage abnormalities, nor is the latter scenario con-

sistent with the summary statement "if our ideas about the genetics are correct, it is likely that Cory's Least Bitterns will turn up from time to time" (Pittaway and Burke 1996).

Aware of the potential for confusion between mutation and true polymorphism, Ford (1945) states that "any given gene subject to adverse selection must always be infrequent in the population; because being constantly eliminated, it is dependent for its existence upon mutation." Therefore, contrary to Pittaway and Burke's (1996) speculation, balanced polymorphism does not allow for temporary establishment of morphs but, in fact, demands permanence "in marked contrast to the distribution of rare genes maintained, ultimately, by mutation pressure" (Ford 1945).

Ford (1945) notes, "A balanced polymorphism in which the variation involved is environmental is generally the product of rather exceptional conditions." There is no indication that there is anything exceptional about the environmental conditions in any of the three main foci of records (Ontario, Florida, southeast South America) when compared with the rest of the range (Scott 1892b), nor do these areas have anything obviously in common that would favour the joint expression of this morph in such widely dispersed geographic locations. It should also be noted that the spatial patterns of occurrence observed in Cory's Bittern do not conform to distributional patterns exhibited by any other polymorphic Ardeid (Bent 1926).

A possible explanation for the observed spatial distribution that appears never to have been proposed is that the concentrations of specimens may be, at least in part, an artifact of observer effort. Ashbridge's Marsh, Toronto (now defunct), where most specimens were collected (Fleming 1906), was frequently used for shooting "so that the bird, though of retiring habits, could scarcely have chosen a more frequented piece of marsh" (Hubert Brown 1894 quoted in Pittaway and Burke 1996, page 38). With all the specimens in this area collected between 1890 and 1900, plus an additional one in 1913, and a similar pattern of temporal clumping seen in Florida, it seems pertinent to repeat the question first posed by Carpenter (1948): how did the morph evade detection prior to these dates? And given the high value of such specimens, why did their collection stop so abruptly? Thus, while the spatial distribution may conceivably be explained as an artifact of observer effort, it seems that temporal distribution cannot.

A recessive allele theory may be partly consistent with the available data on the rarity of Cory's Bittern, but it fails to explain temporal patterns, plumage variation, and the association with partial leucism. Although a single rare recessive allele might be expected to produce a single rare phenotype, rare but heterogeneous mutations would result in a variety of different but rare phenotypes that would be temporally and perhaps spatially clumped. Observed patterns are thus consistent with recurrent mutations.

More important, regardless of whether mutation or recessive alleles is accepted as an explanation, in neither case are the resultant plumages correctly termed morphs. Consequently the basic premise of Pittaway and Burke's (1996) rare recessive allele theory, even if correct, falls outside the definition of polymorphism (Ford 1955), which excludes "segregation of rare recessives."

Conclusion

Cory's Bittern does not comply with Ford's (1945) definition of polymorphism: it has not been genetically determined, it shows extraordinary phenotypic variation, and it is not present in numbers too great to be due solely to recurrent mutation.

The rarity of these aberrations, coupled with a tendency for observers to label any *Ixobrychus exilis* that exhibits abnormally dark plumage characteristics with the name Cory's Bittern, is responsible for the enormous difficulties faced by those who try to define the plumage characteristics of the "morph." The most familiar phenotype, described by Sibley (2011), and understood today to be the typical Cory's Bittern, unduly generalizes the range of variation exhibited by birds ascribed to Cory's in the literature. The assumption of a single plumage type representing Cory's Bittern is an unfortunate byproduct of a general (if unconscious) acceptance by modern ornithologists that Cory's Bittern is a valid colour morph and, hence, must subscribe to a general form.

Pittaway and Burke (1996) state, "The almost complete disappearance of the Cory's Least Bittern… (are) important losses of genetic diversity and habitat to the Least Bittern." However, if, as seems likely, diverse and potentially unrelated factors, some of which may even be deleterious, are responsible for the variation, then no such loss of important genetic diversity is taking place. The appearance and disappearance of a localized population over a short period of time may be attributed to the lower fitness of such abnormally plumaged individuals (Buckley 1982; Slagsvold *et al.* 1988; Ellegren *et al.* 1997; Rutz *et al.* 2004). Their loss is to be expected.

Consequently, I propose that, following a line of thought that began with Bent (1926) and Carpenter (1948), Cory's Bittern should be viewed as a colloquial name referring to any one of a number of abnormally dark-plumaged and phenotypically heterogeneous Least Bitterns and not as a valid colour morph.

Acknowledgements

I thank Matt Garvey, Andrew Vitz and Jon Greenlaw, who provided information on old records in their states. Rob Clay and Tony Gaston read through the manuscript before submission and provided extremely useful comments. I am extremely grateful to Hugo

Cabral for providing the map for this paper. Two anonymous reviewers greatly improved the manuscript with their thorough revision and comments.

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Received 5 October 2013
Accepted 9 February 2014

Use of a Marsh Dominated by the Introduced European Lake Sedge, *Carex acutiformis*, by Highly Localized Native Butterflies

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Catling, Paul M., and Brenda Kostiuk. 2014. Use of a marsh dominated by the introduced European Lake Sedge, *Carex acutiformis*, by highly localized native butterflies. Canadian Field-Naturalist 128(4): 358–362.

To determine whether native butterflies had colonized a marsh in Ottawa that was entirely dominated by the invasive alien European Lake Sedge (*Carex acutiformis*), we surveyed two adjacent stands of the sedge and surrounding habitats. Dion Skipper (*Euphyes dion*), Mulberry Wing (*Poanes massasoit*), Broad-winged Skipper (*P. viator*), and browns (*Lethe* spp.) were all abundant in the introduced sedge, but absent from surrounding habitats. This is the first report of the use of invasive-dominated wetland by native Canadian butterflies. Reduced nectar resources because of dominance of the invasive species over native nectar-producing plants did not prevent significant colonization. The known restriction of the butterflies to native Lakebank Sedge (*Carex lacustris*) as a larval host plant, but its absence in the area, coupled with dominance of its close relative, European Lake Sedge, provides strong circumstantial evidence of the use of the latter as larval food. This report doubles the number of recently localized native butterflies that have been able to increase their distribution by switching to habitat dominated by invasive plants.

Key Words: Ottawa; invasive alien; European Lake Sedge; *Carex acutiformis*; larval food plant; *Euphyes dion*; *Poanes massasoit*; *Poanes viator*; *Lethe eurydice*; localized butterflies; invasive management; food plant switch

Introduction

Invasive alien plants destroy habitat for butterflies and other native insects by displacing specific food plants. The invasion by Scotch Broom (*Cytisus scoparius* [L.] Link) in southeastern Vancouver Island provides a good example (Baron and Backhouse 1999). On the other hand, invasive plants have vastly increased the abundance of some native insect species that were rare and local only a few decades ago (Catling *et al.* 1998). In all cases of beneficial effects of invasive alien species, which are often dominant, the habitats have been disturbed, early successional or both (e.g., roadsides, old fields).

In the Stony Swamp Conservation Area west and southwest of Bells Corners in the city of Ottawa, an extensive area of sedge marsh is entirely dominated by the invasive alien, European Lake Sedge (*Carex acutiformis* Ehrh.) with scattered trees of Eastern White Cedar (*Thuja occidentalis* L.), Red Maple (*Acer rubrum* L.), and Ash (*Fraxinus* sp.). On 22 July 2013, we noticed that the native North American Dion Skipper butterfly (*Euphyes dion* [W. H. Edwards, 1879]) was common and widespread in this marsh (Figure 1). Use of invasive-dominated wetland by localized (sedentary) native butterflies had not been reported previously. To evaluate the extent of the use of this wetland by the skipper and other marsh butterflies, we completed a short survey, the results of which are reported here.

Study Area

The main marsh, stand 1, is approximately 4.2 ha in extent and is located at 45.3143, -75.8516 in the city of Ottawa. Bounded by Robertson Road on the north and the Trans Canada Trail on the south, it is situated on a plateau of sandstone where water levels were apparently raised leading to the death or partial death of cedar woods and the submergence of open mesic meadow followed by colonization by the European Lake Sedge. The adjacent stand 2, to the north across Robertson Road, at 45.31440, -75.85337, has a treeless open part which is 0.1 ha. It has apparently also undergone an increase in water level and is equally dominated by European Lake Sedge as is the understory of the surrounding ash swamp. The dominance of the introduced sedge in these two adjacent stands is remarkably complete. The plants form a thick thatch of dead material along with dense leaves that reach a height of 1–1.5 m and exclude most light. Indeed over the entire area any other graminoid is extremely rare and other herbs (mostly ferns) account for less than 0.1% of the cover (Catling and Kostiuk 2003, Table 1). The marsh is sometimes dry for much of the year, but filled with water to a depth of 20 cm in spring and early summer.

Methods

To determine the extent to which native butterflies were localized in the area of the introduced sedge, we surveyed the two stands as well as adjacent areas to the north, south, east, and west. This survey was carried out on 24 July 2013 between 10:30 a.m. and 2 p.m.; the temperature was 18–22°C. Half an hour was spent at each of six sampling sites and approximately equal areas of 1.2 ha were sampled at each site. To the north of the European Lake Sedge stands are areas of marsh

FIGURE 1. Extensive marsh in Ottawa dominated by European Lake Sedge (*Carex acutiformis*). Inset: male Dion Skipper (*Euphyes dion*) on leaf of European Lake Sedge. Photo: P. M. Catling.

TABLE 1. Vascular plants, by frequency and percentage cover, recorded in 645-m^2 plots along transects through an open wetland dominated by European Lake Sedge (*Carex acutiformis*), near Bells Corners, Ottawa. Cover is the percentage of leaf surface in 1 m^2 of ground surface; thus, 200% means that 1 m^2 of ground contains 2 m^2 of leaf surface.

Species	Frequency (%)	Cover (%)
European Lake Sedge, *Carex acutiformis* Ehrh.	100	200
Reed Canary Grass, *Phalaris arundinacea* L.	1.70	0.79
Marsh Fern, *Thelypteris palustris* Schott var. *pubescens* (Lawson) Fernald	1.24	0.12
Five-leaved Virginia Creeper, *Parthenocissus quinquefolia* (L.) Planchon ex DC.	1.08	0.10
Red-osier Dogwood, *Cornus sericea* L.	0.46	0.04
White Elm, *Ulmus americana* L.	0.15	0.77
White Birch, *Betula papyrifera* Marshall	0.15	0.77
Willowherb, *Epilobium* sp.	0.15	0.15
Crested Wood Fern, *Dryopteris cristata* (L.) A. Gray	0.15	0.01
Common Elderberry, *Sambucus canadensis* L.	0.15	0.10
Sensitive Fern, *Onoclea sensibilis* L.	0.03	0.03
Northern Lady Fern, *Athyrium filix-femina* (L.) Mertens var. *angustum* (Willdenow) G. Lawson	0.03	0.10

Source: Catling and Kostiuk 2003.

dominated (98%) by Broadleaf Cattail (*Typha latifolia* L.), Reed Canary Grass (*Phalaris arundinacea* L.), and Purple Loosestrife (*Lythrum salicaria* L.) and woodlands. To the south, on the south side of the Trans Canada Trail is marsh strongly dominated by Reed Canary Grass and woodland. To the west on higher ground were dry, open meadows and semi-open woodlands of Jack Pine (*Pinus banksiana* Lamb.), Sugar Maple (*Acer saccharum* Marsh.) and Eastern White Cedar. The meadows were dominated by Awnless Brome (*Bromus inermis* Leyss.), Poverty Oatgrass (*Danthonia spicata* [L.] Beauv. Ex Roem. & Schult.), White Bedstraw (*Galium album* Mill.), Early Goldenrod (*Solidago juncea* Aiton), Tufted Vetch (*Vicia cracca* L.) and Oregano (*Origanum vulgare* L.). The east side was largely woodland with few open areas.

The list of species found (Table 2) underestimates the numbers, because any individuals that could not be accurately identified were not listed. Close-focus binoculars were helpful, and some species were confirmed after capture in nets. Care was taken not to count an individual twice by noting direction of flight and moving quickly along the census path.

TABLE 2. Butterflies recorded in a survey of six adjacent areas in a marsh in Ottawa on 24 July 2013. Numbers are underestimates, because individuals that could not be accurately identified were omitted and extra care was taken not to count an individual twice by noting direction of flight and moving quickly along the census path.

Species	Stand 1	Stand 2	North	South	East	West
Delaware Skipper, *Anatrytone logan logan* (W. H. Edwards 1863)	2	—	—	—	—	—
Common Wood Nymph, *Cercyonis pegala nephele* (W. Kirby 1837)	—	—	1	—	5	7
Clouded Sulphur, *Colias philodice* (Godart 1819)	—		—	—	1	1
Dion Skipper, *Euphyes dion* (W. H. Edwards 1879)	23	6		—	—	
Dun Skipper, *Euphyes vestris metacomet* (T. Harris 1862)	—	2	2	—	2	14
Northern Pearly-eye, *Lethe anthedon* (A. Clark 1936)	—	—	—	—	—	3
Lethe eurydice (L.), Eyed Brown	1	—	—	—		—
Lethe spp.	7	3	—	—	1	—
Viceroy, *Limenitis archippus archippus* (Cramer 1775)	—	1	3	—	—	
Pearl Crescent, *Phycioides tharos tharos* (Drury 1773)	—	—	1	—	—	2
Cabbage White, *Pieris rapae* (L.)	1	1	2	1	1	1
Mulberry Wing, *Poanes massasoit* (Scudder 1863)	7	3	—	—	—	—
Broad-winged Skipper, *Poanes viator* (W. H. Edwards 1865)	5	2	—	—	—	—
Eastern Comma, *Polygonia comma* (T. Harris 1842)	—	—	—	—	1	1
Hickory Hairstreak, *Satyrium caryaevorum* (McDunnough 1942)	—	—	—	—	—	1
Great Spangled Fritillery, *Speyeria cybele cybele* (Fabricius 1775)	2	1	1	1	3	4

Results

The survey revealed 15 species of butterflies (Table 2). Recording of *Lethe* species was confused in the field and the only voucher specimen retained was referable to Eyed Brown (*L. eurydice* [L.]). We have listed the *Lethe* species as one *eurydice* and 11 *Lethe* sp. We believe that the largest source of error occurred with the Dion Skipper, and we suspect that the actual numbers of this fast-flying species were up to twice those recorded because individuals were difficult to observe in waving beds of sedge. The data for other species and other habitats are thought to be reliable. Although the surrounding habitats were not highly productive on the day in question, there are some definite patterns of restriction (Table 2). Mulberry Wing (*Poanes massasoit* [Scudder, 1863]), Broad-winged Skipper (*Poanes viator* [W. H. Edwards, 1865]), browns (*Lethe* sp.) and Dion Skipper were all abundant in the introduced sedge but absent in surrounding habitats. Common Wood-nymph (*Cercyonis pegala nephele* [W. Kirby, 1837]) and Dun Skipper (*Euphyes vestris metacomet* [T. Harris, 1862]) were abundant in field habitats to the east and west, but mostly absent from the marshes.

Discussion

Wetland: a new invasive habitat

Habitats dominated by invasive alien species that are used by more or less sedentary eastern Canadian butterflies (Table 3) include weedy, disturbed areas; old fields; woody second growth; and roadsides. This report is the first case of the use of an invasive-alien-dominated wetland by native Canadian butterflies that have a reputation for sedentary behaviour and are widely reported to be highly localized.

A similar situation occurs in the coastal marshes in New Jersey, where later instar larvae of the Rare Skipper (*Problema bulenta* [Boisduval and Le Conte, 1837]) have been found on Common Reed (*Phrag-*

TABLE 3. Localized native eastern Canadian butterflies that have expanded locally or broadly by switching to habitat dominated by an invasive alien plant that, in most cases, serves as larval food.

Species	Introduced food plant and/or community dominant
Henry's Elfin, *Callophrys henrici* (Grote and Robinson 1867)	Glossy Buckthorn *Frangula alnus* P. Mill. L. (Catling *et al.* 1998)
Common Ringlet, *Coenonympha tullia inornata* (W. H. Edwards 1861)	Kentucky Bluegrass, *Poa pratensis* L. (Eberlie and Hess 1980)
Eastern Tailed Blue, *Cupido comyntas* (Godart 1824)	Clovers (Layberry *et al.* 2014)
Wild Indigo Duskywing, *Erynnis baptisiae* (W. Forbes 1936)	Crownvetch, *Securigera varia* (L.) Lassen (Layberry *et al.* 2014)
Dion Skipper, *Euphyes dion* (W. H. Edwards 1879)	Lesser Pond Sedge, *Carex acutiformis* Ehrh. (this article)
Silvery Blue, *Glaucopsyche lygdamus couperi* (Grote 1873)	Alfalfa, vetches, clovers (Catling and Layberry 2013)
Browns, *Lethe* spp. including *L. eurydice* (L.)	Lesser Pond Sedge (this article)
Mulberry Wing, *Poanes massasoit* (Scudder 1863)	Lesser Pond Sedge (this article)
Broad-winged Skipper, *Poanes viator* (W. H. Edwards 1865)	Lesser Pond Sedge (this article)

mites australis [Cav.] Trin. ex Steud.; Chazal and Hobson 2002), presumably the introduced subspecies *australis*, which dominates some of these marshes (P. Catling personal observation). The strong association of the Broad-winged Skipper with wetlands dominated by Common Reed in New England (Nakamura and Cooper 2005; Stichter 2014) provides another example since it is the European subspecies *australis* that dominates these wetlands (personal observation).

A significant addition to recently localized occupants of invasive habitat

Many butterflies native to Canada switched to introduced plants as larval food before 1900 and have always been considered widespread. Examples included the Black Swallowtail (*Papilio polyxenes* Fabricius, 1775) feeding on Queen Anne's Lace (*Daucus carota* L.), the Clouded Sulphur (*Colias philodice* Godart, 1819) feeding on Alfalfa (*Medicago sativa* L.), the American Copper (*Lycaena phlaeas* [Linnaeus, 1761]) feeding on Sheep Sorrel (*Rumex acetosella* L.), and the Silver Spotted Skipper (*Epargyreus clarus* [Cramer, 1775]) feeding on Black Locust (*Robinia pseudoacacia* L.). Any of these may have been rare and local, but their switch to introduced species occurred so early in the settlement period that their original distributions and food plants were not recorded and remain a mystery.

In other cases, the switch to a new larval food has been more recent, has involved previously localized species, and has sometimes been accompanied by substantial range expansion. Examples include the increase in Henry's Elfin (*Callophrys henrici* (Grote and Robinson) in Eastern Ontario accompanying the invasion of Glossy Buckthorn (Frangula alnus P. Mill., Catling *et al.* 1998) and the similar effect of introduced legumes on the Silvery Blue (*Glaucopsyche lygdamus couperi* Grote, Catling and Layberry 2013; Layberry *et al.* 2014). A switch in food source and spread has been recent in some cases. For example the Wild Indigo Duskywing (*Erynnis baptisiae* (Forbes)) has only recently adopted introduced Purple Crown-Vetch (*Coronilla varia*) and areas dominated by it along highways in eastern Canada (personal observation), although its use of Purple Crown-Vetch in the United States dates back to 1979 (Shapiro 1979). Other Hesperiidae, such as the Hobomok Skipper (*Poanes hobomok* [T. Harris, 1862]), Long Dash (*Polites mystic* [W. H. Edwards, 1863]), Peck's Skipper (*P. peckius* [W. Kirby, 1837]), and Tawny-edged Skipper (*Polites themistocles* [Latreille, 1824]), may have switched to introduced Kentucky Bluegrass (*Poa pratensis* L.) as larval food and colonized areas dominated by it long ago, but information is lacking. Some species of *Erynnis* may also have switched to invasive clovers, but information in eastern Canada is incomplete. Regardless, the four new species occupying wetlands strongly dominated by an invasive plant almost doubles the number of localized butterflies that have recently switched to invasive habitats (Table 3).

Although races that have switched to non-native larval food plants may be much less sedentary than those confined to the native food plants from which they developed, many are still more localized than wandering. This requires more study, but clearly rare and local species have increased and in some cases become widespread and abundant by using an invasive plant habitat.

Potential use of European Lake Sedge as a larval food plant

The butterfly species found to be confined to the invasive-dominated marsh are often very localized and do not wander far from the native broad-leaved sedges that serve as their larval food plant (P. Catling personal observation; Layberry *et al.* 1998). As no native sedges were available in the marsh surveyed, it seems likely that European Lake Sedge was used by larvae as a food plant. Dion Skipper, Broad-winged Skipper, and Appalachian Brown are all reported to use the native Lakebank Sedge (*Carex lacustris* Willd.) as larval food (Layberry *et al.* 1998); Lakebank Sedge is closely related to the introduced European Lake Sedge (Reznicek and Catling 2002). This is the first circumstantial evidence of the use of an introduced sedge as larval food by native Canadian butterflies.

Limitations of domination by European Lake Sedge

In the marsh surveyed, nectar-producing herbs were rare and evidently outcompeted by European Lake Sedge. Swamp Milkweed (*Asclepias incarnata* L.) was sparse over the entire area, but its flowers were much visited by Dion Skippers, Mulberry Wings, and Broad-winged Skippers. Nectar may be a limiting factor, but the apparently high abundance of butterflies indicates that this has not prevented colonization.

Conclusions

We report for the first time the use of wetlands dominated by an invasive alien plant species by native Canadian butterflies with a reputation for sedentary behaviour. Our observations have almost doubled the number of butterfly species that have been able to increase their distribution by switching to habitat dominated by invasive plants. There is circumstantial evidence of the use of an introduced sedge species as larval food by native Canadian butterflies. Limited nectar resources resulting from invasive dominance over native nectar-producing plants did not prevent significant colonization by localized native butterflies.

A number of aspects require further study, including the impact of limited nectar resources, precise determination of the *Lethe* species present in the marsh, and proof of the use of European Lake Sedge as a larval food plant.

Acknowledgements

Ross Layberry and Peter Hall provided helpful reviews of this report. Don Lafontaine kindly checked the identification of voucher specimens.

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Received 28 January 2014
Accepted 13 March 2014

Spiders of the Southern Taiga Biome of Labrador, Canada

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Perry, R. C., J. R. Pickavance, and S. Pardy. 2014. Spiders of the southern Taiga biome of Labrador, Canada. Canadian Field-Naturalist 128(4): 363–376.

Ad hoc collections of spiders were made in August and early September 2003 and pitfall trap collections were conducted from June to October in 2004 and 2005 in southern Labrador. These collections represent the first systematic spider sampling for the most easterly area of mainland Canada. In total, 161 species in 15 families were identified to genus and species and 16 were indeterminate. Of the identified species, 89 were new records for Labrador and, of those, 16 species were new records for the province. In total, 94 species (58.4%) have Nearctic distributions and 67 species (41.6%) are Holarctic. No Palearctic species were found. Our study brings the number of spider species recorded in the province of Newfoundland and Labrador to 377 (213 in Labrador).

Key Words: Arachnids; Spiders; Eastern Canada; Labrador; species distribution

Introduction

The distribution of the flora and fauna of Labrador is largely undocumented, and this is particularly true for spiders. Provincial spider lists have been limited to the Newfoundland portion of the province (Hackman 1954; Pickavance and Dondale 2005), where Paquin *et al.* (2010) reported 361 species; in Labrador, only 124 species have been identified.

The completion of the Trans-Labrador Highway in 2003 created an east–west corridor transecting southern Labrador and allowing access to vast tracts of previously inaccessible old-growth forest (Figure 1). Given the absence of biodiversity data for this territory, under the auspices of the Government of Newfoundland and Labrador, we took advantage of this opportunity to collect and identify spiders and insects in the area. Our work resulted in the first systematically collected data on the diversity of spiders in Labrador, important baseline data to which the results of future studies may be compared.

Study Area

Labrador is the mainland portion of the Canadian province of Newfoundland and Labrador. It is situated in northeastern North America between 52° and 60°N and 56° and 64°W and encompasses approximately 293 000 km^2, about 3% of Canada's total land mass (Anderson 1985). The current Labrador spider fauna likely colonized Labrador after the Wisconsin Glacial Episode (the last retreat of the Laurentide glacier) approximately 24 000 years ago (Dyke *et al.* 2002). The prevailing winds move from west to east and colonization probably occurred primarily through wind dispersal (i.e., ballooning) from elsewhere in North America as well as through introductions associated with the arrival of Europeans on the Labrador coast.

Labrador is contained within two distinct biomes: tundra and taiga. Northern Labrador is found in the tundra biome, while southern Labrador, the area where our sampling occurred, is part of the taiga biome, which is typified by very cold winter temperatures, a lengthier growing season and more precipitation relative to the tundra biome. In general, the soils in the taiga biome are acidic and lack important nutrients such as nitrogen and phosphorus. It is dominated by coniferous trees, especially Balsam Fir (*Abies balsamea* [L.] Miller) and Black Spruce (*Picea mariana* [Miller] Britton, Sterns & Poggenburgh). Paper Birch (*Betula papyrifera* Miller), Trembling Aspen (*Populus tremuloides* Michaux), and American Mountain-Ash (*Sorbus americana* Marshall) are the most common deciduous trees. There are also large expanses of wetlands, especially bogs and fens, as well as numerous rivers, lakes, and ponds. Nested within the taiga biome are seven distinct ecological regions (Meades 1990).We ensured each was represented when spider trap-sampling stations were chosen (Table 1, Figure 1). Descriptions of each ecoregion, based on Meades (1990) follow, along with brief descriptions of sampling sites within each ecoregion.

Forteau Barrens

This ecoregion is located at the southeastern tip of Labrador, near the Strait of Belle Isle (Figure 1). The region is characterized by low hills covered by Black Spruce, slope bogs, and barrens. The area is subject to strong winds, frequent storms, cool, rainy summers, and relatively mild winters. Annual precipitation is about 1000–1250 mm and annual snowfall averages 3.5–4.5 m. July temperatures average 12°C and the growing season ranges between 100 and 120 days. Wet soils and climate limit the growth of trees. Barrens are thickly covered with lichens.

For trap sampling in this ecoregion, we chose an alpine heath with dwarfed black spruce and some boggy areas. Traps were placed in areas with clumps of lichens (*Cladina* spp.), laurels (*Kalmia* spp.), and Labrador Tea (*Rhododendron groenlandicum.*).

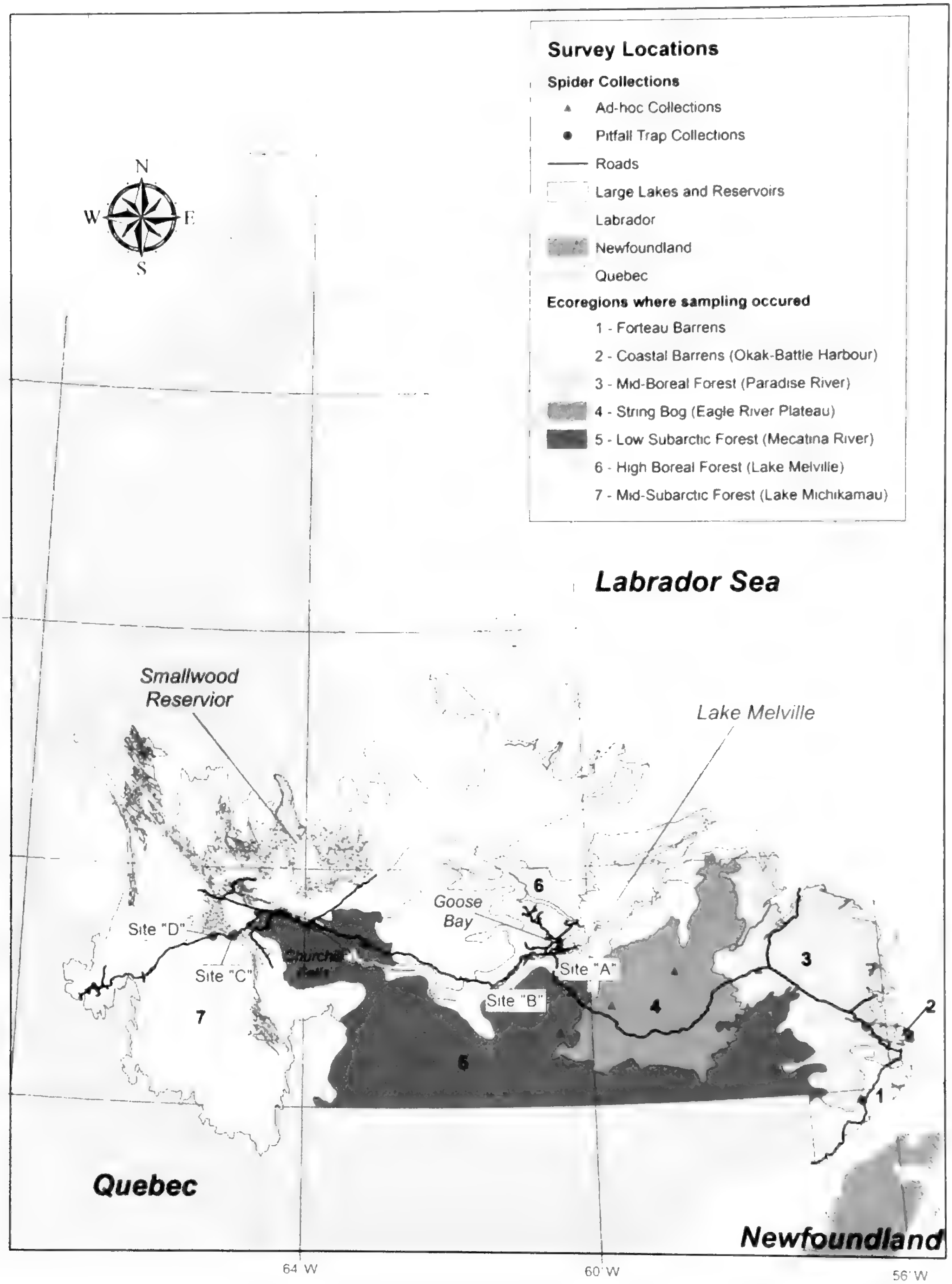

FIGURE 1: Ecoregions and sites where spiders were collected in southern Labrador in 2003 using ad hoc methods (triangles) and in 2004 and 2005 using pitfall traps (circles).

TABLE 1. Locations and ecoregions where spiders were collected using ad hoc methods (2003) and pitfall traps (2004 and 2005) in southern Labrador.

Location (site)	Ecoregion	Longitude, °N	Latitude, °W
Red Bay	Forteau Barrens (1)	56.4069	51.9106
St.Lewis	Coastal Barrens (2)	55.7057	52.3960
Port Hope Simpson	Mid-Boreal Forest (3)	56.2660	52.5185
Muskrat Falls (A)	High Boreal Forest (6)	60.7844	53.2606
Birch Stand (B)	High Boreal Forest (6)	60.9197	53.2294
Middle Brook	Low Subarctic Forest (5)	63.1429	53.3785
Ossak Camp (C)	Mid-Subarctic Forest (7)	65.0129	53.4233
Labrador West (D)	Mid-Subarctic Forest (7)	65.2952	53.4125
Ad hoc site 1	Low Subarctic Forest (5)	60.4374	52.6097
Ad hoc site 2	Low Subarctic Forest (5)	60.2627	52.9495
Ad hoc site 3	String Bog (4)	59.7182	52.8255
Ad hoc site 4	String Bog (4)	58.8275	53.0876
Ad hoc site 5	Mid-Boreal Forest (3)	57.6660	53.056

Coastal Barrens

This ecoregion is found on a narrow band of the coast extending from Napaktok Bay south to the Strait of Belle Isle and containing exposed headlands, some sheltered inlets, and several islands (Figure 1). It has a low subarctic climate with cool summers and a growing season of approximately 100–120 days. Annual precipitation is 1000–1300 mm. Winters are very cold, with an average snowfall of 3.0–4.0 m. The dominant vegetation is *Empetrum* spp., and forest stands occur only in valleys.

Our trap-sampling station was located at the southern end of the ecoregion in a dwarf shrub barren dominated by lichens, some laurels, and Labrador Tea as well as stunted Black Spruce. Traps were placed near boggy sites, in areas with lichen, and at the bottom of rock outcrops.

Mid-Boreal Forest

This ecoregion is located in southeastern Labrador, near the Paradise River (Figure 1). It is characterized by bedrock outcrops and productive, closed-crown forests composed of Black Spruce and Balsam Fir. Hardwoods, such as Paper Birch and Pin Cherry (*Prunus pensylvanica* L. f.), can also be found, as well as raised bogs in valleys. A boreal climate prevails with cool to warm summers, short cold winters, a growing season of 120–140 days, and annual precipitation between 1000 and 1300 mm (mean snowfall 4.0–5.0 m).

In this ecoregion both trap sampling and ad hoc collection were carried out. Trap-sampling plots were located near the town of Port Hope Simpson in mixed stands of Balsam Fir and Black Spruce. Some hardwoods were also present. Traps were set in moss.

String Bog

This ecoregion corresponds largely with the Eagle River Plateau, which is 500–600 m above sea level and consists of extensive string bogs containing numerous open pools surrounded by fen vegetation. Summers are cool and winters are very cold. Annual precipitation is 1000–1200 mm (mean snowfall approximately 5.0 m). Vegetation in the area consists of scrub black spruce, Labrador Tea, and Splendid Feather Moss (*Hylocomium splendens* [Hedw.] Schimp. in B.S.G.). Sporadic eskers support open lichen woodlands dominated by Black Spruce. Speckled Alder (*Alnus incana* [L.] Moench) can be found along most watercourses and lakes. Only ad hoc sampling of spiders was done in this ecoregion.

Low Subarctic Forest

This ecoregion, located primarily in southern Labrador, is characterized by broad river valleys and rolling hills covered by shallow till, drumlins, and eskers. Summers are short and cool and winters are long and very cold. The growing season is approximately 120–140 days and annual precipitation is 1000–1300 mm (annual snowfall 3.5–5.0 m). Open Black Spruce forests are the dominant vegetation. String bog complexes cover extensive areas throughout the region.

Ad hoc and trap sampling were done in this ecoregion. The trap-sampling site was an open Black Spruce forest with a thick mat of lichens covering the forest floor. Understory plants included Labrador Tea, laurels, and other small shrubs. Traps were set in the lichens and often did not penetrate into the soil because of the thickness of the lichens.

High Boreal Forest

This ecoregion encompasses the Churchill River valley and the coastal plain surrounding Lake Melville (Figure 1). Alluvial soils can be found in river terraces, while the uplands have shallow, well-drained soils. Summers are cool and winters very cold. The growing season is 120–140 days, and annual precipitation is 800–1100 mm. Annual snowfall averages approximately 4.0 m. Forests in the area have closed canopies and are highly productive. Richer slopes contain Balsam Fir, Paper Birch, and Trembling Aspen. Black Spruce is present in most stands and dominates upland areas and lichen woodlands. Ribbed fens and plateau bogs occur in upland depressions and coastal plains, respectively.

In this ecoregion we chose two trap-sampling sites, characterized by different types of vegetation. The first was near the town of Goose Bay, on the branch road to Muskrat Falls (Site A, Figure 1). The area consists of large sand hills with intermittent Black Spruce and large areas of *Cladina* spp. Traps were placed in open sandy and lichen-dominated areas. The second site, also located close to Goose Bay, was on a southeast facing slope dominated by hardwoods, such as Paper Birch, Red Maple (*Acer rubrum* L.), Pin Cherry and Trembling Aspen (Site B, Figure 1). The understory contained clubmosses (*Lycopodium* spp.), broom mosses (*Dicranum* spp.), ferns, small Red Alders (*Alnus rubra* Bongard), American Mountain-Ash, and a thick layer of leaf litter.

Mid-Subarctic Forest:

This ecoregion encompasses the upland plateaus of central and western Labrador and is characterized by eskers and drumlin ridges. The climate is continental and subarctic with cool, short summers and long, cold winters. The growing season is 100–120 days, annual precipitation is 900–1110 mm, and annual snowfall averages 4.0 m. White Spruce (*Picea glauca* [Moench] Voss) dominates in the north, Black Spruce elsewhere in this ecoregion. Trembling Aspen, open lichen woodlands, and, in areas with flat topography, string bog complexes surrounded by Black Spruce– sphagnum forests are also characteristic of the area.

In this ecoregion two sites with different types of vegetation were chosen for trap sampling. The first, near the Ossakmanuan Reservoir (Site C, Figure 1), was dominated by closed-canopy Black Spruce/*Kalmia* and Black Spruce/*Cladina*, with some leaf litter and mosses also present. The second sampling site was in a recently severely burned forest near Labrador City (Site D, Figure 1). Most of the trees were fire killed, and a thin layer of charred humus remained on the ground. Some areas were beginning to be colonized by Blueberry (*Vaccinium* L. spp.), laurels, and mosses.

Methods

Sampling

Ad hoc collections (random, non-systematic collection of spiders by hand) were carried out between 7 August and 3 September 2003, before construction of the last phase of the Trans-Labrador Highway, as preliminary surveys at two sites in each of the String Bog and Low Subarctic Forest ecoregions and one site in the Mid-Boreal Forest ecoregion (Figure 1). They were conducted by two survey teams of four Newfoundland government conservation officers. Each person was directed to look for spiders by exploring shorelines, turning over rocks, and examining plants and debris during their spare time. When found, spiders were placed in sample jars and preserved with ethyl alcohol.

Trap sampling was conducted in the summers of 2004 and 2005 between early June and early October. In 2004, the Forteau Barrens, Coastal Barrens, Mid-Boreal Forest and Mid-Sub Arctic Forest ecoregions were sampled. In 2005, collections were made in the High Boreal Forest and Low Subarctic Forest ecoregions (Figure 1).

Pitfall traps were placed at eight sites in the six ecoregions (Table 1). Sampling sites were chosen based on whether they contained vegetation typical for an ecoregion. At each site, seven plots were established, each containing 10 pitfall traps (for a total of 70 traps per site and 560 for the entire study) placed in a circle with a diameter of about 10 m. Samples were retrieved from pitfall traps at each site from one to seven times (average four), depending on weather conditions and collector schedules, from June through early October. Collecting was done by regional biologists from the Wildlife Division, Department of Environment and Conservation, and conservation officers from the Department of Natural Resources, Government of Newfoundland and Labrador.

Each pitfall trap consisted of a 10-cm diameter flower pot (450 mL volume) set in the ground. An ice cream sundae cup (250 mL) was half filled with propylene glycol and placed in the flower pot. This system allowed for simple collection of contents and resetting of traps. Each trap was covered with a white plastic card held in place with four large nails (Spence and Niemelä 1994) to exclude rainwater. Samples from each plot were placed in a single jar, labeled by plot and site number.

Spider sorting and curation

Specimens and other materials were removed from the collected samples using a sieve. Spiders were then separated and placed, with data labels, in clean vials containing 95% ethanol. The spiders were subsequently sent for identification to Memorial University of Newfoundland and Labrador.

Checklist

Specimens that could not be identified are shown as indeterminate in the checklist and housed for future examination at either The Rooms Provincial Museum (marked NF in the checklist) or at the Canadian National Collection of Insects and Arachnids, Agriculture and Agri-Food Canada, Ottawa (marked CNC). If they have been catalogued, a number is also listed.

Species nomenclature follows Platnick (2014). The number of species identified in each family is given in parentheses after each family heading. Collection locality is expressed as numbers 1 through 7, corresponding to the ecoregions (Figure 1). Ecoregions 6 and 7 each contained two sampling sites and, therefore, location is further divided into A and B or C and D, respectively. Collection dates are presented as month and day. The total number of each species is presented, separated into male (♂) and female (♀) specimens. Comments are primarily limited to general species distribution (Holarctic or Nearctic). In some instances,

comments also include species abundance and state whether the record is new for Labrador or the entire province.

Results

In total, ad hoc and trap-sampling collections produced 14 964 spider specimens (including indeterminates) representing 161 species in 15 families (see checklist and Table 2). The five ad hoc collections produced 136 spiders representing 29 species in 11 families (73 of these were immature and identified only to family). Nineteen species were represented by only a single specimen. From the pitfall trap samples, 14 901 specimens were collected, representing 147 species in 15 families.

Checklist of Labrador Spiders

AGELENIDAE (1 SPP.)
Agelenopsis utahana (Chamberlin & Ivie, 1933)
Ecoregions: 6A
Collection date: Sept. 13
Total samples: ♀ = 1, ♂ = 1
Comment: Nearctic; new record for Labrador

AMAUROBIIDAE (5 SPP.)
Arctobius agelenoides (Emerton, 1919)
Ecoregions: 5, 7C
Collection dates: July 18; Oct. 8
Total samples: ♀ = 1, ♂ = 1
Comment: Nearctic; new record for both the province and Eastern Canada

Callobius bennetti (Blackwall, 1846)
Ecoregion: 6B
Collection dates: June 17; July 4, 5; Aug. 3, 12, 25; Sept. 13
Total samples: ♀ = 17, ♂ = 41
Comment: Nearctic

Callobius nomeus (Chamberlin, 1919)
Ecoregions: 5, 6A
Collection date: Aug. 25
Total samples: ♀ = 3, ♂ = 1
Comment: Nearctic

Cybaeopsis euopla (Bishop & Crosby, 1935)
Ecoregions: 1, 2, 3, 5, 6A and B, 7C
Collection dates: June; July; Aug.; Sept.; Oct.
Total samples: ♀ = 52, ♂ = 82
Comment: Nearctic; good representation across all sampling stations

Cybaeopsis tibialis (Emerton, 1888)
Ecoregion: 6A and B
Collection dates: June 17; July 4; Aug. 3, 12; Oct. 27.
Total samples: ♀ = 32, ♂ = 2
Comment: Nearctic; majority (31) found at site B

ARANEIDAE (8 SPP. AND 1 INDETERMINATE)
Araneus nordmanni (Thorell, 1870)
Ecoregion: 4
Collection date: Aug. 3
Total samples: ♀ = 1, ♂ = 1
Comment: Holarctic

Araneus saevus (L. Koch, 1872)
Ecoregion: 6B
Collection date: Sept. 13
Total samples: ♀ = 1, ♂ = 0
Comment: Holarctic

Araneus trifolium (Hentz, 1847)
Ecoregion: 2
Collection date: Aug. 7
Total samples: ♀ = 1, ♂ = 0
Comment: Nearctic

Araneus sp. Clerck, 1757 (indeterminate; NF)
Ecoregion: 3
Collection date: Aug. 25
Total samples: ♀ = 0, ♂ = 1

TABLE 2: Orders and composition of the spider fauna sampled by ad hoc (2003) and pitfall trap (2004 and 2005) collection in southern Labrador.

Family	Nearctic	Holarctic	Introduced	Total species	% of total
Agelenidae	1	0	0	1	0.6
Amaurobiidae	5	0	0	5	3.1
Araneidae	2	6	0	8	5.0
Clubionidae	2	2	0	4	2.5
Dictynidae	2	2	0	4	2.5
Gnaphosidae	5	11	0	16	9.9
Hahniidae	3	1	0	4	2.5
Linyphiidae	50	30	0	80	49.7
Liocranidae	0	1	0	1	0.6
Lycosidae	9	6	0	15	9.3
Philodromidae	2	2	0	4	2.5
Salticidae	3	0	0	3	1.9
Tetragnahidae	1	1	0	2	1.2
Theridiidae	3	1	0	4	2.5
Thomisidae	5	5	0	10	6.2
Total	93	68	0	161	100

Araniella displicata (Hentz, 1847)
Ecoregion: 3
Collection date: Aug. 25
Total samples: ♀ = 1, ♂ = 0
Comment: Holarctic

Araniella proxima (Kulczynski, 1885)
Ecoregion: 6B
Collection date: Aug. 3
Total samples: ♀ = 0, ♂ = 1
Comment: Holarctic; new record for Labrador

Cyclosa conica (Pallas, 1772)
Ecoregion: 4
Collection date: Aug. 7
Total samples: ♀ = 1, ♂ = 0
Comment: Holarctic

Hypsosinga rubens (Hentz, 1847)
Ecoregion: 6A
Collection date: July 5
Total samples: ♀ = 0, ♂ = 1
Comment: Nearctic; new record for Labrador

Larinioides patagiatus (Clerck, 1757)
Ecoregion: 4
Collection dates: Aug. 7; Sept. 3
Total samples: ♀ = 2, ♂ = 1
Comment: Holarctic

CLUBIONIDAE (4 SPP.)

Clubiona bryantae Gertsch, 1941
Ecoregion: 1
Collection dates: Aug. 6, 23; Sept. 7; Oct. 26
Total samples: ♀ = 9, ♂ = 6
Comment: Nearctic; new record for Labrador

Clubiona canadensis Emerton, 1890
Ecoregions: 1, 2, 3, 6B, 7C and D
Collection dates: June 17; July 4, 11, 22; Aug. 5, 6, 10, 25
Total samples: ♀ = 7, ♂ = 16
Comment: Nearctic

Clubiona kulczynskii Lessert, 1905
Ecoregions: 1, 2, 5, 6B, 7D
Collection dates: July 4, 5, 11, 22; Aug. 3, 6, 25
Total samples: ♀ = 6, ♂ = 5
Comment: Holarctic

Clubiona trivialis C. L. Koch, 1843
Ecoregions: 1, 2, 6A, 7D
Collection dates: June 17; Aug. 1, 6, 25; Sept. 7; Oct. 26
Total samples: ♀ = 5, ♂ = 3
Comment: Holarctic

DICTYNIDAE (4 SPP.)

Dictyna brevitarsa Emerton, 1915
Ecoregion: 2
Collection date: Aug. 7
Total samples: ♀ = 0, ♂ = 1
Comment: Nearctic; new record for Labrador

Emblyna annulipes (Blackwall, 1846)
Ecoregion: 2
Collection date: Aug. 7
Total samples: ♀ = 1, ♂ = 0
Comment: Holarctic

Emblyna manitoba (Ivie, 1947)
Ecoregions: 4, 5
Collection date: Aug. 7
Total samples: ♀ = 1, ♂ = 1
Comment: Holarctic; new record for the province

Hackmania prominula (Tullgren, 1948)
Ecoregions: 6A, 7C
Collection dates: July 5, 19; Aug. 13, 29
Total samples: ♀ = 0, ♂ = 18
Comment: Nearctic; new to Eastern Canada and the province

GNAPHOSIDAE (16 SPP.)

Drassodes mirus Platnick and Shadab, 1976
Ecoregion: 2
Collection dates: July 22; Aug. 10; Oct. 27
Total samples: ♀ = 1, ♂ = 3
Comment: Nearctic; new record for the province

Drassodes neglectus (Keyserling, 1887)
Ecoregions: 2, 6A
Collection dates: June 17; July 5, 11, 22
Total samples: ♀ = 1, ♂ = 4
Comment: Holarctic; new record for Labrador

Gnaphosa borea Kulczynski, 1908
Ecoregions: 1, 2, 3, 4, 5, 6A, 7C and D
Collection dates: June; July; Aug.; Sept.; Oct.
Total samples: ♀ = 109, ♂ = 365
Comment: Holarctic; the large majority were found in ecoregion 3 in July

Gnaphosa brumalis Thorell, 1875
Ecoregions: 2, 7C and D
Collection dates: July 11, 22; Aug. 1, 29
Total samples: ♀ = 7, ♂ = 31
Comment: Nearctic; the majority came from ecoregion 7, site D

Gnaphosa microps Holm, 1939
Ecoregions: 1, 2, 3, 5, 6A and B, 7C and D
Collection dates: June; July; Aug.; Sept.; Oct.
Total samples: ♀ = 49, ♂ = 100
Comment: Holarctic; the majority were found in ecoregion 7, sites C and D

Gnaphosa muscorum (L. Koch, 1866)
Ecoregions: 1, 2, 3, 4, 5, 6A and B, 7D
Collection dates: June; July; Aug.; Sept.; Oct.
Total samples: ♀ = 70, ♂ = 215
Comment: Holarctic; the majority were found in ecoregion 6, site A and ecoregion 7, site D

Gnaphosa parvula Banks, 1896
Ecoregion: 1
Collection dates: Aug. 6, 7, 23; Sept. 7
Total samples: ♀ = 1, ♂ = 5
Comment: Nearctic; new record for Labrador

Haplodrassus eunis Chamberlin, 1922
Ecoregions: 5, 6A
Collection dates: June 17; July 5, 19; Aug. 3, 25
Total samples: ♀ = 24, ♂ = 70
Comment: Nearctic; only one specimen from ecoregion 5; new record for the province

Haplodrassus hiemalis (Emerton, 1909)
Ecoregion: 2
Collection dates: July 22; Aug. 25; Sept. 7; Oct. 4, 27
Total samples: ♀ = 0, ♂ = 5
Comment: Holarctic; new record for Labrador

Haplodrassus signifer (C. L. Koch, 1839)
Ecoregions: 1, 2, 3, 5, 6A, 7C and D
Collection dates: June 17; July 4, 5, 11, 18, 20, 22; Aug 1, 2, 29; Oct. 8
Total samples: ♀ = 49, ♂ = 66
Comment: Holarctic; the majority came from ecoregion 7, site D; new record for Labrador

Micaria aenea Thorell, 1871
Ecoregions: 3, 5, 6A and B
Collection dates: June 17; July 4, 5, 19, 22; Sept. 13
Total samples: ♀ = 46, ♂ = 30
Comment: Holarctic. The majority (70) were found in ecoregion 6, site A; new record for Labrador

Micaria constricta Emerton, 1894
Ecoregion: 7D
Collection dates: July 11; Aug. 1
Total samples: ♀ = 0, ♂ = 3
Comment: Holarctic

Micaria pulicaria (Sundevall, 1831)
Ecoregions: 1, 2, 3, 5, 6A, 7D
Collection dates: June; July; Aug.; Sept.
Total samples: ♀ = 23, ♂ = 19
Comment: Holarctic; new record for Labrador

Orodrassus canadensis Platnick & Shadab, 1975
Ecoregion: 5
Collection date: Aug. 7
Total samples: ♀ = 0, ♂ = 1
Comment: Nearctic

Zelotes fratris Chamberlin, 1920
Ecoregions: 2, 3, 5, 6A
Collection dates: June; July; Aug.; Sept.; Oct.
Total samples: ♀ = 25, ♂ = 50
Comment: Holarctic; the majority were found in ecoregions 5 and 6

Zelotes sula Lowrie and Gertsch, 1955
Ecoregions: 6A, 7C
Collection dates: July 19; Aug. 3, 25, 29
Total samples: ♀ = 0, ♂ = 4
Comment: Holarctic

HAHNIIDAE (4 SPP.)

Cryphoeca montana Emerton, 1909
Ecoregions: 5, 6B
Collection dates: June 17; July 4, 5, 19, 22; Aug. 1
Total samples: ♀ = 5, ♂ = 55
Comment: Nearctic

Hahnia cinerea Emerton, 1890
Ecoregion: 6A
Collection date: June 17
Total samples: ♀ = 0, ♂ = 1
Comment: Nearctic; new record for Labrador

Hahnia glacialis Sørenson, 1898
Ecoregions: 1, 2, 3, 7C and D
Collection dates: July; Aug.; Sept.; Oct.
Total samples: ♀ = 78, ♂ = 124
Comment: Holarctic; specimens were plentiful at all of the listed sites

Neoantistea magna (Keyserling, 1887)
Ecoregions: 2, 3, 5, 6B, 7C and D
Collection dates: June; July; Aug.; Sept.; Oct.
Total samples: ♀ = 383, ♂ = 511
Comment: Nearctic; specimens were plentiful at all of the listed sites

LINYPHIIDAE (80 SPP. AND 15 INDETERMINATE)

Agyneta allosubtilis Loksa, 1965
Ecoregions: 1, 3, 6A
Collection dates: June 17; July 5, 11, 19, 22, Aug. 7, 23; Sept. 7
Total samples: ♀ = 8, ♂ = 30
Comment: Holarctic

Agyneta dynica Saaristo & Koponen, 1998
Ecoregion: 2
Collection date: July 22
Total samples: ♀ = 0, ♂ = 2
Comment: Nearctic; new record for Labrador

Agyneta olivacea (Emerton, 1882)
Ecoregions: 1, 2; 5, 6A and B, 7C and D
Collection dates: June; July; Aug.; Sept.; Oct.
Total samples: ♀ = 129, ♂ = 139
Comment: Holarctic; the majority were found in ecoregions 5 and 6, site A; new record for Labrador

Agyneta simplex (Emerton, 1926)
Ecoregions: 1, 2, 3, 5, 6A, 7C and D
Collection dates: June; July; Aug.; Sept.; Oct.
Total samples: ♀ = 52, ♂ = 172
Comment: Nearctic; only 13 specimens from the combined sites at ecoregions 1, 2, and 3; new record for Labrador

Allomengea dentisetis (Grube, 1861)
Ecoregion: 6B
Collection dates: Aug. 12, 25; Sept. 13
Total samples: ♀ = 1, ♂ = 2
Comment: Holarctic

Bathyphantes eumenis (L. Koch, 1879)
Ecoregions: 1, 2, 3, 6B, 7C and D
Collection dates: July; Aug.; Sept.; Oct.
Total samples: ♀ = 12, ♂ = 10
Comment: Holarctic

Bathyphantes pallidus (Banks, 1892)
Ecoregions: 3, 6A and B, 7C
Collection dates: June; July; Aug.; Sept.
Total samples: ♀ = 91, ♂ = 44
Comment: Nearctic; the majority were found in ecoregion 6, site A; only two were found at site B

Carorita limnaea (Crosby & Bishop, 1927)
Ecoregion: 6A
Collection dates: June 17; July 5, 19; Aug. 3
Total samples: ♀ = 0, ♂ = 13
Comment: Holarctic; new record for Labrador

Centromerus longibulbus (Emerton, 1882)
Ecoregions: 1, 5, 7C
Collection dates: June 17; July 11, 20
Total samples: ♀ = 0, ♂ = 5
Comment: Nearctic; new record for Labrador

Centromerus sylvaticus (Blackwall, 1841)
Ecoregions: 3, 6B
Collection dates: Aug. 25; Sept. 13, 27; Oct. 27
Total samples: ♀ = 13, ♂ = 23
Comment: Holarctic

Ceraticelus atriceps (O. P.-Cambridge, 1874)
Ecoregions: 1, 2, 7C and D
Collection dates: Aug. 1, 23; Sept. 7
Total samples: ♀ = 4, ♂ = 1
Comment: Nearctic

Ceraticelus crassiceps Chamberlin & Ivie, 1939
Ecoregions: 1, 3
Collection dates: Aug. 10, 23; Sept. 7; Oct. 27
Total samples: ♀ = 5, ♂ = 2
Comment: Nearctic

Ceraticelus fissiceps (O. P.-Cambridge, 1874)
Ecoregions: 5, 6A and B
Collection dates: June; July; Aug.; Sept.
Total samples: ♀ = 17, ♂ = 3
Comment: Nearctic

Ceratinella brunnea Emerton, 1882
Ecoregions: 1, 2, 3, 5, 6A
Collection dates: June; July; Aug.; Sept.; Oct.
Total samples: ♀ = 28, ♂ = 4
Comment: Nearctic

Ceratinella ornatula (Crosby & Bishop, 1925)
Ecoregion: 7D
Collection date: July 11
Total samples: ♀ = 0, ♂ = 1
Comment: Nearctic

Cnephalocotes obscurus (Blackwall, 1834)
Ecoregions: 3, 6A, 7D
Collection dates: June; July; Aug.; Sept.
Total samples: ♀ = 27, ♂ = 27
Comment: Holarctic; new record for the province

Diplocentria bidentata (Emerton, 1882)
Ecoregions: 1, 3, 5, 6A and B, 7C and D
Collection dates: June; July; Aug.; Sept.; Oct.
Total samples: ♀ = 63, ♂ = 295
Comment: Holarctic; good representation from all sites in listed ecoregions; new record for Labrador

Diplocentria rectangulata (Emerton, 1915)
Ecoregions: 2, 5, 6A and B, 7C and D
Collection dates: June; July; Aug.; Sept.; Oct.
Total samples: ♀ = 45, ♂ = 205
Comment: Holarctic; large majority sampled from ecoregion 5; new record for Labrador

Diplocentria retinax (Crosby & Bishop, 1936)
Ecoregion: 6A
Collection dates: June 17; July 5
Total samples: ♀ = 1, ♂ = 3
Comment: Nearctic; new record for the province

Diplocephalus subrostratus (O. P.-Cambridge, 1873)
Ecoregion: 6B
Collection dates: June 17; July 5, 19; Aug. 3, 12, 25
Total samples: ♀ = 19, ♂ = 27
Comment: Holarctic; new record for Labrador

Erigone blaesa Crosby & Bishop, 1928
Ecoregions: 4, 5
Collection date: Aug. 7
Total samples: ♀ = 0, ♂ = 2
Comment: Nearctic

Estrandia grandaeva (Keyserling, 1886)
Ecoregions: 3, 6B
Collection dates: July 19; Aug. 5
Total samples: ♀ = 1, ♂ = 1
Comment: Holarctic

Gonatium crassipalpum Bryant, 1933
Ecoregions: 1, 2, 3, 5, 6A, 7C and D
Collection dates: June; July; Aug.; Sept.; Oct.
Total samples: ♀ = 68, ♂ = 62
Comment: Nearctic; well represented in all sampled ecoregions

Grammonota angusta Dondale, 1959
Ecoregions: 2, 5, 6A
Collection dates: June 17; Aug. 7; Sept. 13; Oct. 27
Total samples: ♀ = 7, ♂ = 0
Comment: Nearctic

Helophora insignis (Blackwall, 1841)
Ecoregions: 2, 3, 6B, 7C
Collection dates: June; July; Aug.; Sept.; Oct.
Total samples: ♀ = 15, ♂ = 14
Comment: Holarctic

Hilaira herniosa (Thorell, 1875)
Ecoregions: 1, 2, 3, 5, 6A, 7C
Collection dates: June; July; Aug.; Sept.; Oct.
Total samples: ♀ = 103, ♂ = 75
Comment: Holarctic; well represented at all sites in listed ecoregions

Hybauchenidium gibbosum (Sørenson, 1898)
Ecoregions: 3; 5; 6, Sites A and B; 7, Site C
Collection dates: July 5, 18, 19, 22; Aug. 3; Sept. 13, 27; Oct. 27
Total samples: ♀ = 8, ♂ = 2
Comment: Holarctic

Improphantes complicatus (Emerton ,1882)
Ecoregions: 1, 2, 3, 5, 6A and B, 7C and D
Collection dates: June; July; Aug.; Sept.; Oct.
Total samples: ♀ = 49, ♂ = 54
Comment: Holarctic

Incestophantes washingtoni (Zorsch, 1937)
Ecoregions: 1, 2, 3, 4, 6B, 7C and D
Collection dates: June; July; Aug.; Sept.; Oct.
Total samples: ♀ = 30, ♂ = 3
Comment: Nearctic

Islandiana flaveola (Banks, 1892)
Ecoregion: 6A
Collection date: June 17
Total samples: ♀ = 0, ♂ = 1
Comment: Nearctic; new record for Labrador

Islandiana sp. Braendegaard, 1932 (indeterminate; NF)
Ecoregions: 1, 5, 7D
Collection dates: June 17; July 11, 20
Total samples: ♀ = 2, ♂ = 5

Lepthyphantes alpinus (Emerton, 1882)
Ecoregions: 1, 2, 3, 5, 6A and B, 7C
Collection dates: June; July; Aug.; Sept.; Oct.
Total samples: ♀ = 57, ♂ = 24
Comment: Holarctic; new record for Labrador

Lepthyphantes turbatrix (O. P.-Cambridge, 1877)
Ecoregion: 6A
Collection date: Aug. 12
Total samples: ♀ = 1, ♂ = 0
Comment: Nearctic; new record for Labrador

Lepthyphantes sp. Menge, 1866 (indeterminate; CNC #7)
Ecoregions: 5, 6A and B
Collection date: June 17
Total samples: ♀ = 0, ♂ = 7

Macrargus multesimus (O. P.-Cambridge, 1875)
Ecoregions: 3, 6A
Collection dates: June 17; Aug. 25; Sept. 13; Oct. 27
Total samples: ♀ = 8, ♂ = 0
Comment: Holarctic; new record for the province

Maro amplus Dondale & Buckle, 2001
Ecoregion: 6B
Collection date: June 17
Total samples: ♀ = 0, ♂ = 8
Comment: Nearctic; new record for Labrador

Maro nearcticus Dondale & Buckle, 2001
Ecoregion: 6B
Collection date: June 17
Total samples: ♀ = 0, ♂ = 2
Comment: Nearctic; new record for Labrador

Mermessus entomologicus (Emerton, 1911)
Ecoregion: 3
Collection date: July 22
Total samples: ♀ = 0, ♂ = 1
Comment: Nearctic; new record for Labrador

Mermessus trilobatus (Emerton, 1882)
Ecoregion: 6A
Collection dates: July 5, 19
Total samples: ♀ = 0, ♂ = 3
Comment: Holarctic; new record for Labrador

Mermessus undulatus (Emerton, 1914)
Ecoregion: 1
Collection dates: July 20; Aug. 23
Total samples: ♀ = 0, ♂ = 2
Comment: Nearctic; new record for Labrador

Metopobactrus prominulus (O. P.-Cambridge, 1872)
Ecoregion: 6A
Collection date: July 5
Total samples: ♀ = 0, ♂ = 1
Comment: Holarctic; new record for the Province

Microlinyphia mandibulata (Emerton, 1882)
Ecoregions: 3, 7C
Collection date: Sept. 27
Total samples: ♀ = 4, ♂ = 0
Comment: Nearctic; new record for Labrador

Microneta viaria (Blackwall, 1841)
Ecoregion: 6A
Collection date: June 17
Total samples: 2 (sex not reported)
Comment: Holarctic; new record for the province

Oreoneta brunnea (Emerton, 1882)
Ecoregions: 1, 2
Collection dates: July 20; Aug. 25; Sept. 7; Oct. 26
Total samples: ♀ = 26, ♂ = 24
Comment: Nearctic; new record for Labrador

Oreoneta sp. Kulcynski, 1894 (indeterminate; NF 167)
Ecoregion: 7D
Collection date: July 11
Total samples: ♀ = 0, ♂ = 1

Oreonetides flavescens (Crosby, 1937)
Ecoregion: 6A
Collection date: June 17
Total samples: ♀ = 0, ♂ = 2
Comment: Nearctic; new record for Labrador

Oreonetides vaginatus (Thorell, 1872)
Ecoregions: 1, 2, 3, 5, 6B, 7C and D
Collection dates: June; July; Aug.; Sept.; Oct
Total samples: ♀ = 6, ♂ = 11
Comment: Holarctic

Oreophantes recurvatus (Emerton, 1913)
Ecoregion: 3
Collection date: Oct. 27
Total samples: ♀ = 0, ♂ = 2
Comment: Nearctic

Pelecopsis mengei (Simon, 1884)
Ecoregions: 3, 6B
Collection dates: June; July; Aug.; Sept.; Oct.
Total samples: ♀ = 19, ♂ = 9
Comment: Holarctic; only one spider collected from ecoregion 3; new record for Labrador

Pelecopsis moesta (Banks, 1892)
Ecoregion: 6A
Collection date: July 5
Total samples: ♀ = 0, ♂ = 1
Comment: Nearctic; new record for the province

Pityohyphantes subarcticus Chamberlin & Ivie, 1943
Ecoregions: 1, 2, 3, 4, 5, 6A, 7C
Collection dates: June; July; Aug.; Sept.; Oct.
Total samples: ♀ = 14, ♂ = 3
Comment: Nearctic

Pocadicnemis americana Millidge, 1976
Ecoregions: 1, 2, 3, 5, 6A, 7C and D
Collection dates: June; July; Aug.; Sept.; Oct.
Total samples: ♀ = 392, ♂ = 405
Comment: Nearctic; 11 came from ecoregions 1, 2, and 3

Pocadicnemis pumila (Blackwall, 1841)
Ecoregion: 6B
Collection date: June 17
Total samples: ♀ = 0, ♂ = 1
Comment: Nearctic; new record for the province

Poeciloneta calcaratus (Emerton, 1909)
Ecoregions: 1, 3, 4
Collection dates: Aug. 7, 23; Oct. 27
Total samples: ♀ = 1, ♂ = 2
Comment: Nearctic

Satilatlas sp. Keyserling, 1886 (indeterminate; NF)
Ecoregions: 3, 7D
Collection date: July 11
Total samples: ♀ = 0, ♂ = 3

Satilatlas sp. Keyserling, 1886 (indeterminate; NF)
Ecoregion: 3
Collection dates: July 22; Sept. 7
Total samples: ♀ = 2, ♂ = 0

Sciastes truncatus (Emerton, 1882)
Ecoregions: 3, 5, 6A and B, 7C and D
Collection dates: June; July; Aug.; Sept.; Oct.
Total samples: ♀ = 39, ♂ = 26
Comment: Nearctic; new record for Labrador

Scironis tarsalis (Emerton, 1911)
Ecoregion: 6B
Collection dates: June 17; July 5; Sept. 13
Total samples: ♀ = 3, ♂ = 8
Comment: Nearctic; new record for Labrador

Scotinotylus alpinus (Banks, 1896)
Ecoregion: 3
Collection dates: Sept. 7; Oct. 27
Total samples: ♀ = 0, ♂ = 2
Comment: Nearctic; new record for the province

Scotinotylus sacer (Crosby, 1929)
Ecoregions: 3, 5, 7C and D
Collection dates: June 17; July 11; Aug. 1, 24, 29; Sept. 7; Oct. 8
Total samples: ♀ = 6, ♂ = 11
Comment: Holarctic; new record for Labrador

Semljicola obtusus (Emerton, 1915)
Ecoregion: 1
Collection date: July 20
Total samples: ♀ = 1, ♂ = 0
Comment: Nearctic; new record for Labrador

Sisicottus montanus (Emerton, 1882)
Ecoregions: 1, 6B, 7D
Collection dates: June 17; July 11, 20; Aug. 6; Oct. 26, 27
Total samples: ♀ = 5, ♂ = 6
Comment: Nearctic; new record for Labrador

Sisicus penifusifer Bishop & Crosby, 1938
Ecoregion: 6A
Collection date: July 5
Total samples: ♀ = 2, ♂ = 0
Comment: Nearctic; new record for Labrador

Sisis rotundus (Emerton, 1925)
Ecoregions: 5, 6A, 7C
Collection dates: June 17; July 11, 18; Aug. 1, 29
Total samples: ♀ = 12, ♂ = 7
Comment: Nearctic

Stemonyphantes blauveltae Gertsch, 1951
Ecoregion: 2
Collection dates: Aug. 2, 10, 25; Oct. 27
Total samples: ♀ = 3, ♂ = 6
Comment: Nearctic; new record for Labrador

Styloctetor stativus (Simon, 1881)
Ecoregions: 5, 6A and B, 7C and D
Collection dates: June 17; July 4, 5, 11; Aug. 1, 2, 3, 29
Total samples: ♀ = 9, ♂ = 47
Comment: Holarctic; new record for Labrador

Tapinocyba bicarinata (Emerton, 1913)
Ecoregions: 1, 7C
Collection dates: July 11, 20; Aug. 1, 29
Total samples: ♀ = 1, ♂ = 7
Comment: Nearctic; new record for Labrador

Tapinocyba prima Dupérré & Paquin, 2005
Ecoregions: 5, 6A, 7C and D
Collection dates: June; July; Aug.
Total samples: ♀ = 3, ♂ = 61
Comment: Nearctic; new record for Labrador

Tapinocyba simplex (Emerton, 1882)
Ecoregions: 1, 5, 6A and B
Collection dates: June; July; Aug.
Total samples: ♀ = 17, ♂ = 5
Comment: Nearctic; new record for Labrador

Tapinocyba sp. Simon, 1884 (indeterminate; CNC)
Ecoregion: 6A
Collection date: Aug. 3
Total samples: ♀ = 1, ♂ = 0

Tunagyna debilis (Banks, 1892)
Ecoregions: 1, 2, 5, 6A and B, 7C and D
Collection dates: June; July; Aug.; Sept.; Oct.
Total samples: ♀ = 14, ♂ = 31
Comment: Holarctic; new record for Labrador

Wabasso cacuminatus Millidge, 1984
Ecoregions: 1, 2, 7C and D
Collection dates: July 11, 20, 22; Aug. 1, 6, 29; Oct. 8, 27
Total samples: ♀ = 22, ♂ = 18
Comment: Holarctic; new record for Labrador

Walckenaeria arctica Millidge, 1983
Ecoregions: 1, 2, 3, 5, 7C and D
Collection dates: June; July; Aug.; Sept.; Oct.
Total samples: ♀ = 39, ♂ = 22
Comment: Nearctic; new record for Labrador

Walckenaeria atrotibialis (O. P.-Cambridge, 1878)
Ecoregions: 5, 6A and B, 7C
Collection dates: June; July; Aug.; Sept.
Total samples: ♀ = 51, ♂ = 46
Comment: Holarctic; new record for Labrador

Walckenaeria castanea (Emerton, 1882)
Ecoregions: 1, 2, 3, 5, 6A, 7C and D
Collection dates: June; July; Aug.; Oct.
Total samples: ♀ = 21, ♂ = 27
Comment: Nearctic

Walckenaeria clavipalpis Millidge, 1983
Ecoregion: 1
Collection date: Aug. 6
Total samples: ♀ = 1, ♂ = 0
Comment: Nearctic; new record for Labrador

Walckenaeria communis (Emerton, 1882)
Ecoregions: 1, 2, 3, 5, 6A and B, 7C and D
Collection dates: June; July; Aug.; Sept.; Oct.
Total samples: ♀ = 160, ♂ = 33
Comment: Nearctic; new record for Labrador

Walckenaeria cuspidata brevicula (Crosby & Bishop, 1931)
Ecoregion: 1
Collection date: Sept. 7
Total samples: ♀ = 1, ♂ = 0
Comment: Nearctic; new record for Labrador

Walckenaeria directa (O. P.-Cambridge, 1874)
Ecoregions: 1, 3, 5, 6A and B, 7D
Collection dates: June; July; Aug.; Sept.; Oct.
Total samples: ♀ = 43, ♂ = 9
Comment: Nearctic

Walckenaeria exigua Millidge, 1983
Ecoregions: 2, 3, 5, 6A and B, 7C and D
Collection dates: June; July; Aug.; Sept.; Oct.
Total samples: ♀ = 15, ♂ = 200
Comment: Nearctic; new record for Labrador

Walckenaeria karpinskii (O. P.-Cambridge, 1873)
Ecoregions: 5, 6A, 7C and D
Collection dates: June 17; July 4, 11, 18; Aug. 2; Sept. 12
Total samples: ♀ = 6, ♂ = 5
Comment: Holarctic; new record for Labrador

Walckenaeria lepida (Kulczynski, 1885)
Ecoregion: 4
Collection date: Aug. 7
Total samples: ♀ = 0, ♂ = 1
Comment: Holarctic; new record for Labrador

Walckenaeria spiralis (Emerton, 1882)
Ecoregions: 1, 2, 5, 6A, 7C and D
Collection dates: June; July; Aug.; Oct.
Total samples: ♀ = 1, ♂ = 50
Comment: Holarctic; new record for Labrador

Walckenaeria tricornis (Emerton, 1882)
Ecoregions: 1, 3, 5, 6A and B, 7C and D
Collection dates: June; July; Aug.; Sept.
Total samples: ♀ = 50, ♂ = 179
Comment: Nearctic; one found in September, but the vast majority were collected in June, July, and at the beginning of August

Wubana pacifica (Banks, 1896)
Ecoregion: 3
Collection date: Sept. 13
Total samples: ♀ = 0, ♂ = 1
Comment: Nearctic; new record for Labrador

Zornella armata (Banks, 1906)
Ecoregions: 1, 3, 6A, 7C
Collection dates: June 17; Sept. 27; Oct. 26, 27
Total samples: ♀ = 22, ♂ = 7
Comment: Nearctic; new record for Labrador
Indeterminate; NF 158

Ecoregion: 1
Collection date: July 20
Total samples: ♀ = 0, ♂ = 1
Indeterminate; NF 159

Ecoregion: 1
Collection date: July 20
Total samples: ♀ = 1, ♂ = 0
Indeterminate; NF 160

Ecoregion: 3
Collection date: Oct. 27
Total samples: ♀ = 1, ♂ = 0
Indeterminate; NF 161

Ecoregion: 3
Collection date: Oct. 27
Total samples: ♀ = 1, ♂ = 0
Indeterminate; NF 162

Ecoregion: 6A
Collection date: July 19
Total samples: ♀ = 1, ♂ = 0
Indeterminate; NF 163

Ecoregion: 1
Collection date: July 20
Total samples: ♀ = 1, ♂ = 0
Indeterminate; NF 164

Ecoregion: 3
Collection date: July 22
Total samples: ♀ = 1, ♂ = 0
Indeterminate; NF 165

Ecoregion: 7D
Collection date: July 11
Total samples: ♀ = 1, ♂ = 0
Indeterminate; NF 166

Ecoregion: 6A
Collection date: June 17
Total samples: ♀ = 1, ♂ = 0

LIOCRANIDAE (1 SPP.)
Agroeca ornata Banks, 1892
Ecoregions: 1, 2, 3, 5, 6A and B, 7C and D
Collection dates: June; July; Aug.; Sept.; Oct.
Total samples: ♀ = 71, ♂ = 56
Comment: Holarctic; new record for Labrador

LYCOSIDAE (15 SPP.)
Alopecosa aculeata (Clerck, 1757)
Ecoregions: 1, 2, 3, 5, 6A and B, 7C and D
Collection dates: June; July; Aug.; Sept.; Oct.
Total samples: ♀ = 95, ♂ = 272
Comment: Holarctic

Arctosa alpigena (Doleschall, 1852)
Ecoregions: 1, 2, 5, 7C and D
Collection dates: July 11, 20; Aug. 1, 29, 23; Sept. 7; Oct. 8, 27
Total samples: ♀ = 82, ♂ = 48
Comment: Holarctic

Arctosa raptor (Kulczynski, 1885)
Ecoregion: 1
Collection dates: July 20; Aug. 6
Total samples: ♀ = 4, ♂ = 18
Comment: Holarctic; new record for Labrador

Arctosa rubicunda (Keyserling, 1877)
Ecoregion: 3
Collection dates: Aug. 25; Sept. 13
Total samples: ♀ = 2, ♂ = 0
Comment: Nearctic; new record for Labrador

Hogna frondicola (Emerton, 1885)
Ecoregions: 3, 6A
Collection dates: June17; July 5, 19, 22; Aug. 25; Sept. 13
Total samples: ♀ = 8, ♂ = 3
Comment: Nearctic; new record for Labrador

Pardosa concinna (Thorell, 1877)
Ecoregions: 1, 2, 3, 5, 7C and D
Collection dates: June; July; Aug.; Sept.; Oct.
Total samples: ♀ = 124, ♂ = 256
Comment: Nearctic

Pardosa furcifera (Thorell, 1875)
Ecoregions: 1, 2
Collection dates: July 20, 22; Aug. 6, 23; Sept. 7, 17; Oct. 26, 27
Total samples: ♀ = 297, ♂ = 326
Comment: Nearctic

Pardosa fuscula (Thorell, 1875)
Ecoregions: 1, 3, 7C
Collection dates: July 20, 22; Aug. 6, 23, 25; Sept. 27; Oct. 26
Total samples: ♀ = 12, ♂ = 7
Comment: Nearctic

Pardosa hyperborea (Thorell, 1872)
Ecoregions: 1, 2, 3, 5, 6A, 7C and D
Collection dates: June; July; Aug.; Sept.; Oct.
Total samples: ♀ = 1143, ♂ = 2401
Comment: Holarctic

Pardosa mackenziana (Keyserling, 1877)
Ecoregions: 1, 3, 5, 6A and B
Collection dates: June 17; July 5, 20, 22; Aug. 3, 5
Total samples: ♀ = 26, ♂ = 72
Comment: Nearctic; new record for Labrador

Pardosa uintana Gertsch, 1933
Ecoregions: 1, 2, 3, 4, 5, 6A and B, 7C and D
Collection dates: June; July; Aug.; Sept.; Oct.
Total samples: ♀ = 439, ♂ = 572
Comment: Nearctic

Pardosa xerampelina (Keyserling, 1877)
Ecoregions: 5, 6B, 7D
Collection dates: June 17; July 11; Aug. 1; Oct. 8
Total samples: ♀ = 7, ♂ = 26
Comment: Nearctic

Pirata bryantae Kurata, 1944
Ecoregions: 1, 3, 5, 6A and B, 7C and D
Collection dates: June; July; Aug.; Oct.
Total samples: ♀ = 181, ♂ = 560
Comment: Nearctic

Pirata piraticus (Clerck, 1757)
Ecoregion: 3
Collection date: Sept. 13
Total samples: ♀ = 1, ♂ = 0
Comment: Holarctic; new record for Labrador

Trochosa terricola Thorell, 1856
Ecoregions: 3, 5, 6A and B, 7C and D
Collection dates: June; July; Aug.; Sept.
Total samples: ♀ = 73, ♂ = 106
Comment: Holarctic

PHILODROMIDAE (4 SPP.)
Philodromus alascensis Keyserling, 1884
Ecoregion: 7D
Collection date: July 11
Total samples: ♀ = 1, ♂ = 0
Comment: Holarctic

Philodromus placidus Banks, 1892
Ecoregion: 6A
Collection date: July 5
Total samples: ♀ = 0, ♂ = 1
Comment: Nearctic

Philodromus rufus quartus Dondale & Redner, 1968
Ecoregions: 5, 6B
Collection dates: June 17; July 4
Total samples: ♀ = 2; ♂ = 0
Comment: Nearctic

Thanatus formicinus (Clerck, 1757)
Ecoregions: 1, 2, 3, 7D
Collection dates: July 11, 22; Aug. 1, 10, 25, 29; Sept. 7, 13; Oct. 27
Total samples: ♀ = 17, ♂ = 30
Comment: Holarctic; new record for Labrador

SALTICIDAE (3 SPP.)
Evarcha hoyi (Peckham & Peckham, 1883)
Ecoregions: 5, 6B
Collection dates: July 18, 19
Total samples: ♀ = 1, ♂ = 1
Comment: Nearctic; new record for Labrador

Neon nelli Peckham & Peckham, 1888
Ecoregion: 6A and B
Collection dates: June 17; July 4, 5, 19; Aug. 3, 12, 25
Total samples: ♀ = 25, ♂ = 29
Comment: Nearctic

Talavera minuta (Banks, 1895)
Ecoregion: 6A
Collection date: July 5
Total samples: ♀ = 0, ♂ = 1
Comment: Nearctic; new record for the province

TETRAGNAHIDAE (2 SPP.)
Tetragnatha elongata Walckenaer, 1841
Ecoregion: 5
Collection date: Aug. 7
Total samples: ♀ = 1, ♂ = 0
Comment: Nearctic and Neotropical; new record for Labrador

Tetragnatha extensa (Linnaeus, 1758)
Ecoregion: 5
Collection date: Aug. 7
Total samples: ♀ = 0, ♂ = 1
Comment: Holarctic

THERIDIIDAE (4 SPP.)
Enoplognatha intrepida (Sørenson, 1898)
Ecoregion: 2
Collection dates: Aug. 10, 25; Sept. 7; Oct. 27
Total samples: ♀ = 1, ♂ = 16
Comment: Nearctic; new record for Labrador

Robertus fuscus (Emerton, 1894)
Ecoregions: 2, 3, 5, 6B, 7C and D
Collection dates: June 17; July 5; Aug. 25; Sept. 7, 17; Oct. 27
Total samples: ♀ = 7, ♂ = 15
Comment: Nearctic

Rugathodes sexpunctatus (Emerton, 1882)
Ecoregion: 7D
Collection date: Aug. 1
Total samples: ♀ = 0, ♂ = 1
Comment: Holarctic; new record for Labrador

Theonoe stridula Crosby, 1906
Ecoregions: 5, 6A, 7C and D
Collection dates: June 17; July 4, 5, 11, 19; Aug. 3, 29; Oct. 8
Total samples: ♀ = 7, ♂ = 42
Comment: Nearctic; new record for Labrador

THOMISIDAE (10 SPP.)
Misumena vatia (Clerck, 1757)
Ecoregion: 1
Collection date: July 20
Total samples: ♀ = 0, ♂ = 1
Comment: Holarctic

Ozyptila sincera canadensis Dondale & Redner, 1975
Ecoregions: 2, 3
Collection dates: Aug. 5, 25; Sept. 13, 27
Total samples: ♀ = 9, ♂ = 1
Comment: Nearctic; new record for Labrador

Xysticus canadensis Gertsch, 1934
Ecoregions: 3, 6A and B, 7C
Collection dates: June 17; July 5, 11; Aug. 29; Oct. 27
Total samples: ♀ = 2, ♂ = 12
Comment: Holarctic

Xysticus durus (Sørenson, 1898)
Ecoregion: 7
Collection date: Aug. 1
Total samples: ♀ = 1, ♂ = 0
Comment: Nearctic; new record for the province

Xysticus ellipticus Turnbull, Dondale & Redner, 1965
Ecoregions: 2, 3
Collection dates: July 22; Oct. 27
Total samples: ♀ = 0, ♂ = 15
Comment: Nearctic; new record for the Province

Xysticus emertoni Keyserling, 1880
Ecoregions: 1, 2, 3, 5, 6A and B, 7D
Collection dates: June 17; July 4, 5, 11, 22; Aug. 1, 5, 10; Oct. 27
Total samples: ♀ = 6, ♂ = 50
Comment: Holarctic; new record for Labrador

Xysticus keyserlingi Bryant, 1930
Ecoregions: 1, 2, 3, 5, 7D
Collection dates: July; Aug.; Sept.; Oct.
Total samples: ♀ = 30, ♂ = 90
Comment: Nearctic; new record for Labrador

Xysticus luctuosus (Blackwall, 1836)
Ecoregions: 1, 2, 3, 7D
Collection dates: July; Aug.; Sept.; Oct.
Total samples: ♀ = 5, ♂ = 40
Comment: Holarctic; new record for Labrador

Xysticus obscurus Collett, 1877
Ecoregion: 3
Collection date: Aug. 7
Total samples: 3 (sex unknown)
Comment: Holarctic

Xysticus triguttatus Keyserling, 1880
Ecoregions: 1, 2, 3
Collection dates: July 22; Aug. 5; Oct. 26, 27
Total samples: ♀ = 2, ♂ = 14
Comment: Nearctic; new record for Labrador

Discussion

Origins of the Labrador spider fauna

Most (58.4%) of the species identified in this study have Nearctic distributions; however, a significant Holarctic component was also present (41.6%) (Table 2). Noticeably absent from the collections were introduced species or ones previously known only from Palearctic or other regions.

The frequency of Holarctic species increases as one moves further north in the Nearctic region (Pickavance and Dondale 2005) and our data appear to support this. Of spider species reported for the island of Newfoundland (primarily south of our study area), 33% have Holarctic distributions (Pickavance and Dondale 2005). In a more northerly locality, subarctic and arctic Quebec, the percentage of spider species with Holarctic distribution is nearly 50% (Koponen 1994). Still further north, on Belcher Island, the proportion rises to 58% (Koponen 1992).

Introduced species

The absence of introduced species in this study may be attributed to a combination of factors. First, most of the sample sites were in relatively pristine old-growth forests in remote locations. Collection sites near communities were still well outside town boundaries. Also, the population of Labrador is approximately 29 000, and species introductions may be less likely to occur there than in more heavily populated areas elsewhere. The severe cold of Labrador winters may also limit the colonization and spread of more southerly exotics. With the creation of the new Trans-Labrador Highway, species introductions may increase and it will be interesting to continue to monitor spider diversity in the study area to examine influences of the new highway on species introductions.

Noteworthy occurrences

In total, 161 species were identified in this collection, 89 of which are new records for Labrador. Of the 89 new species, 16 species are new records for the province. The former species complement reported for Labrador was 124 (Paquin *et al.* 2010); our addition of 89 species raises the new species total to 213. For the province, the total number of spider species has been raised to 395: 361 (Newfoundland total) + 18 (reported only in Labrador) + 16 (new records).

Of the 16 species records new to the province, almost all can be found as far east as Quebec or New Brunswick and, therefore, it is not surprising that they can be found in Newfoundland and Labrador. However, a few stand out as noteworthy. The collection of *Arctobius agelenoides* (Amaurobiidae) is of interest because, in the Nearctic region, this has been considered a western species (Marusik and Koponen 2005) recorded in Canada from Yukon, Northwest Territories, Nunavut, British Columbia, Alberta, Saskatchewan, and Manitoba (Paquin *et al.* 2010). *Arctobius agelenoides* may have a continuous distribution across Canada or perhaps the Labrador population is disjunct.

Hackmania prominula (Dictynidae) is relatively rarely encountered. It is a northern Holarctic species previously reported in western North America from Alaska, Yukon, British Columbia, Alberta, Saskatchewan, and Manitoba (Paquin *et al.* 2010). Our Labrador records are the first for eastern North America.

Haplodrassus eunis (Gnaphosidae) is primarily a western species with records from Alaska to California and eastward to the Great Lakes (Platnick and Dondale 1992). Our report indicates that its distribution extends throughout the North of the Neararctic region Our record of *Gnaphosa parvula* also extends this species range across the north of the Nearctic region.

Agyneta dynica (Linyphiidae) is a rarely collected Nearctic endemic reported in Canada only from Yukon, subarctic Quebec, and on parts of the subarctic barrens of the Northern Peninsula of Newfoundland (Pickavance and Dondale 2005; Paquin *et al.* 2010; Dupérré 2013). Our Labrador record helps define the true distribution of this species.

With the addition of 89 species, the total known species complement for Labrador stands at 213. It is

likely that this total is not yet complete; much of Labrador remains to be surveyed. In addition, this survey was largely confined to the ground and, therefore, spiders that make their homes in trees and shrubs are most likely underrepresented. Further, this collection was confined to lower elevations in the southerly latitudes of Labrador. To reveal the full species complement of the northern fauna, further sampling is still required north of 54° latitude and at higher elevations.

Acknowledgements

We are indebted to Dr. Jaime Pinzon, Dr. Robert Bennett and an anonymous reviewer whose editorial comments and shared knowledge were invaluable in the completion of this work. We thank conservation officer Chuck Porter, senior biologist Rebecca Jeffery, and field technician Ted Pardy for routinely collecting our pitfall trap samples. We also thank Dara Walsh for sorting and collating the collection and Carl Marks for his global information system contributions. Finally, we would like to thank the many natural resource officers who participated in the initial ad hoc survey; their efforts ultimately inspired the completion of the larger survey.

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Received 30 January 2014
Accepted 28 March 2014

Morphological and Ecological Variation among Populations and Subspecies of Burbot (*Lota lota* [L, 1758]) from the Mackenzie River Delta, Canada

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Recknagel, Hans, Amy Amos, and Kathryn R. Elmer. 2014. Morphological and ecological variation among populations and subspecies of Burbot (*Lota lota* [L, 1758]) from the Mackenzie River Delta, Canada. Canadian Field-Naturalist 128(4): 377–384.

The Burbot (*Lota lota* [L, 1758]) is a holarctic distributed freshwater fish in the Gadidae family. In northwestern Canada, it has an important value for local and traditional fisheries. We describe the morphology and ecology of Burbot from four populations in the Mackenzie River Delta. Two subspecies come into contact in this area, which is the western edge of *Lota lota maculosa* distribution (one population in our study) and the eastern edge of *Lota lota lota* distribution (three populations in our study). We found the combined length weight relationship in these four populations to be $\log_{10}(\text{weight}) = -3.986 + 2.617 * \log_{10}(\text{length})$. There was no difference in mean body length (overall mean and standard deviation 73.4 ± 8.7 cm), although the *L. l. lota* populations were heavier than the *L. l. maculosa* population. All populations differed in their carbon and nitrogen stable isotope signatures ($\delta^{15}N$ overall mean 12.1 ± 1.59; $\delta^{13}C$ overall mean −25.54 ± 1.11). Main prey items were four fish species: Ninespine Stickleback (*Pungitius pungitius* [L, 1758]), Broad Whitefish (*Coregonus nasus* [Pallas, 1776]), Burbot, and Northern Pike (*Esox lucius* [L, 1758]). Ecological and morphological differences may be due to local conditions and population variability or to the different *Lota lota* subspecies. More ecological and morphological information from this region is needed to resolve possible phenotypic differences between the subspecies.

Key Words: Burbot; *Lota lota*; Mackenzie River; weight–length relationship; sexual dimorphism; ecological variation; parapatric subspecies; freshwater fish; loche

Introduction

The Burbot (*Lota lota* [L, 1758]) is a northern fish species with a circumpolar distribution in freshwater rivers, creeks, and lakes. Burbot live in cold lakes and rivers, where they tend to frequent deep water near the bottom (McPhail and Paragamian 2000). They can attain a length of 1 m and a weight of 8 kg, although most fish are 0.3–0.6 m in length and weigh 1–3 kg (McPhail and Paragamian 2000). The Mackenzie River Delta (Northwest Territories, Canada) is one of the northernmost ranges of Burbot distribution. In this area, they are fished for their liver and eggs, which are their most valued parts (Gwich'in Elders 1999). Recently, there have been increased reports of Burbot with malformations, poor muscle tone, unpleasant tasting flesh, and diseased livers from local and traditional fishers in the Gwich'in Settlement Area (Thompson 2008). This prompted research by the Gwich'in Renewable Resources Board, the data from which are the basis of this study.

Burbot are great dispersers and individuals may cover extensive geographic areas, perhaps driven by spawning behaviour and the search for food (McPhail and Paragamian 2000; Slavík *et al.* 2005). Their spawning period ranges from winter (December) until early spring (March), when water is often still covered by ice (Gwich'in Elders 1999; McPhail and Paragamian 2000). Little is known about spawning behaviour in nature, but it seems to be polygynous broadcast spawning, as Burbot form spawning aggregations where a few females are surrounded by many males (McCrimmon 1959). There is no evidence of sex-biased dispersal based on population genetic analyses (Elmer *et al.* 2012). Whether Burbot have defined home ranges depends on their habitat. In lakes, Burbot do not keep stable positions as food availability is low and dispersed, whereas, in rivers, higher food availability permits them to occupy defined home ranges (Slavík *et al.* 2005). Burbot home ranges are much bigger than those of other temperate freshwater fish, with measured movements of up to 255 km (McPhail and Paragamian 2000).

There are two subspecies of Burbot: *Lota lota maculosa* is restricted to North America and *Lota lota lota* is distributed across Eurasia and Beringia. Based on population genetic analyses, Elmer *et al.* (2012) located a precise contact zone between Burbot subspecies in the Mackenzie River Delta. At Tsiigehtchic (included in the current study), most individuals collected were *L. l. maculosa* and upriver of that locality only *L. l. maculosa* were found. Downstream from Tsiigehtchic, all populations in the Mackenzie River Delta were exclusively *L. l. lota*. Therefore, the lower Mackenzie River is where the discrete parapatric distributions of

the Burbot subspecies meet at a narrow contact zone and there is very little hybridization.

Some biologists consider the two subspecies to be morphologically variable. The subspecies may differ in caudal peduncle ratio, the size of the pectoral fins, and the number of pyloric caeca (e.g., Pivnicka 1970; McPhail and Paragamian 2000), but some authors (e.g., McPhail and Lindsey 1970; Scott and Crossman 1973) have declined to distinguish subspecies because supposedly diagnostic traits are highly variable. Weight is thought to differ between fish from lentic and lotic environments and possibly between the two subspecies as well (Fisher *et al.* 1996). The causes for this morphological variation are not clear (McPhail 1997). To some extent, the variation might be a result of repeated isolation in refugia during multiple glacial cycles, which led to different genetic lineages and even subspecies (Van Houdt *et al.* 2005; Elmer *et al.* 2008). Morphological differences between fluvial and lacustrine Burbot have also been observed and led to the conclusion that lotic and lentic morphologies may be adapted to alternative contemporary niches (McPhail 1997). To date, there is a dearth of information about the morphological, meristic, and ecological variability of this wide-ranging species and, unfortunately, much of it is only available in grey literature (e.g., McPhail 1997; although see recent research advances by Cott *et al.* 2013a,b).

In this study, we describe and compare aspects of ecological differentiation and morphological variability among Burbot populations in the Mackenzie River Delta. As the two subspecies abut in this zone (Elmer *et al.* 2008, 2012) and there is little or no information available about possible ecological and reproductive barriers between subspecies (McPhail 1997), our aim was to assess variability in body size and weight, gonadosomatic index, and ecology (trophic niche and diet) and highlight possible areas for future research.

Study Area

Burbot were caught during winter 2007 and 2008 by line hooking at four traditional Burbot fishing locations in the Mackenzie River Delta by Gwich'in community fish monitors (Table 1, Figure 1). In Inuvik, two localities were fished: at Bombadeer Creek downstream from a sewage lagoon and at Sam Arey's Creek just upstream. In Aklavik, all fish were collected from Jackfish Creek, across from town. In Tsiigehtchic, Burbot were mostly collected from the Arctic Red River but some were captured from the Mackenzie River within 10 km of Tsiigehtchic. For Fort McPherson, all locations were Peel River tributary creeks (Woody Elias Creek, Basook Creek, Nelson Creek, Husky River Creek, Hudson Bay Creek, Rotten Eye Creek) within 50 km of Fort McPherson.

Methods

Total length was measured to the nearest millimetre. Wet weight of each fish was taken to the nearest gram. Stomachs were weighed and examined for species of macrofauna by a Gwich'in Renewable Resources Board technician. Gonads were extracted and weighed for fecundity analysis using the gonadosomatic index (GSI = [gonad weight/body weight] × 100). Fish ages were inferred from otoliths by A.A. in 2007 and under contract by North/South Consultants Inc. in 2008. A muscle tissue sample was collected and stable isotope measurements were taken by Environment Canada using mass spectrometry.

Statistical analyses

We tested whether morphological (weight and length) and ecological characteristics (stable isotopes, stomach content) differed among populations using analysis of covariance (ANCOVA) with age and sex as covariates to correct for age-specific differences and sexual dimorphism. Stomach content data were first transformed into a contingency table and then analyzed using a generalized linear model and a χ^2 test with prey type as a covariate. In case a characteristic differed significantly among populations, all populations were contrasted using generalized linear models, setting sex and age as fixed effects as they are likely to influence morphological and ecological characteristics (i.e., older fish are usually larger, diet may shift during ontogeny, etc.) to determine which populations differed from each other. In these pairwise population comparisons, we corrected for multiple testing by using the Bonferroni correction. We conducted statistical analyses in R version 3.0.2 open-source programming language. We pooled individual data by population to compare means and standard deviations. We calculated weight–length relationships using weight in grams and length in milli-

TABLE 1. Sampling location and dates for Burbot subspecies (*Lota lota lota* and *L. l. maculosa*) collected from four populations in the Mackenzie River Delta, Northwest Territories, Canada.

Population*	*n*	Latitude, °N	Longitude, °W	Collection dates
Lota lota lota				
Inuvik	94	68.4	133.9	Feb. and May 2007, Jan. and Feb. 2008
Aklavik	133	68.3	134.9	Nov. 2007, Jan. 2008
Fort McPherson	137	67.7	134.7	Nov. 2007, Feb. 2008
Lota lota maculosa				
Tsiigehtchic	28	67.4	133.8	Nov. 2007

*Subspecies inferred from Elmer *et al.* (2012).

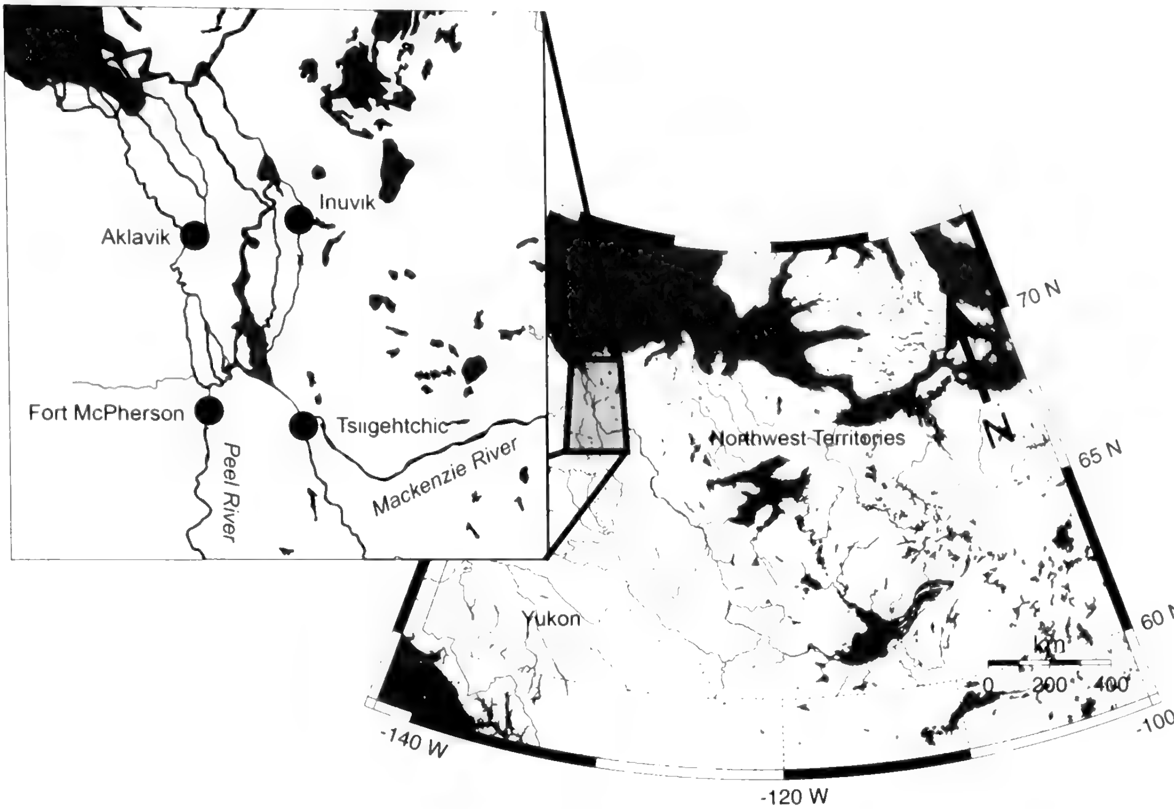

FIGURE 1. Sampling locations (black dots) for Burbot subspecies (*Lota lota lota* and *L. l. maculosa*) in the Mackenzie River Delta, Northwest Territories, Canada.

metres across all populations (following Fisher *et al.* 1996). We compared GSI for the two sexes using ANOVA.

Results

Age

The individuals in our samples were mostly older adults (mean age 13.6 years) (Table 2). Mean ages were approximately equal across populations, except for the Tsiigehtchic population, which was older (mean 14.9 years, range 9–25 years, $F = 3.559$, $P = 0.0176$; Table 2). The age difference was significant only between the Fort McPherson and Tsiigehtchic populations ($t = 3.221$, $P = 0.0018$). Therefore, our ecological and morphological analyses are unlikely to be influenced by varying age effects across populations; however, we performed subsequent statistical analyses with age as a covariate.

Sexual dimorphism

Across all populations, female and male Burbot differed significantly in weight and length, females being longer (mean [± standard deviation] 757 ± 82 mm versus 683.4 ± 72 mm, $F = 10.15$, $P = 0.002$) and heavier (mean 3699 ± 1240 g versus 2785 ± 891 g, $F = 13.16$, $P = 0.0005$) than males. Diet did not differ significantly between the sexes, as indicated by stomach contents ($F = 3.82$, $P = 0.35$) and stable isotope (δ^{15}N: $F = 1.65$, $P = 0.20$; δ^{13}C: $F = 0.24$, $P = 0.63$) analyses. Mean GSI differed significantly between the sexes ($F = 303.69$, $P < 0.0001$), and was on average 5.66 ± 1.58 ($n = 245$) for mature females and 11.26 ± 4.26 ($n = 84$) for mature males (Table 2).

Morphological variation across populations

Body length differed significantly across populations ($F = 10.51$, $P < 0.0001$). Mean length was less in the Tsiigehtchic population (707.5 ± 73.8 mm) compared with the other three populations (Aklavik 731.3 ± 78.0 mm, Fort McPherson 726.5 ± 97.3 mm, Inuvik 748.7 ± 86.3 mm), but only Fort McPherson and Aklavik ($t = -3.762$, $P = 0.0003$) and Inuvik and Fort McPherson ($t = -3.428$, $P = 0.0009$) differed significantly from each other after Bonferroni correction (Tables 2 and 3).

Weight differed significantly between populations ($F = 20.37$, $P < 0.0001$) and ranged from 2471.0 ± 829.2 g in Tsiigehtchic up to 3523.9 ± 1304.0 g in Inuvik (Table 2). The Tsiigehtchic population had the lowest mean weight and, overall, three of the six pairwise comparisons of weight were significantly different (Table 3).

TABLE 2. Characteristics of Burbot subspecies (*Lota lota lota* and *L. l. maculosa*) collected from four populations in the Mackenzie River Delta, Northwest Territories, Canada.

Population	Length, mean mm (SD)	Weight, mean g (SD)	Age, mean years (SD)	Female GSI	Male GSI	$\delta^{13}C$, mean (SD)	$\delta^{15}N$, mean (SD)
Lota lota lota							
Inuvik	748.7 (86.3)	3523.9 (1304.0)	13.3 (2.3)	6.11 (1.23)	12.38 (2.58)	−24.49 (0.87)	13.43 (1.32)
Aklavik	731.3 (78.0)	3473.0 (1112.8)	13.7 (2.0)	5.65 (1.44)	12.32 (4.22)	−26.03 (1.05)	12.73 (1.34)
Fort McPherson	726.5 (97.3)	3419.5 (1269.3)	13.2 (2.4)	5.42 (1.70)	10.55 (3.79)	−26.02 (0.86)	11.33 (1.21)
Lota lota maculosa							
Tsiigehtchic	707.5 (73.8)	2471.0 (829.2)	14.9 (4.0)	4.30 (3.13)	7.91 (5.99)	−25.11 (1.06)	12.17 (1.75)
All	732.4 (8.8)	3391.0 (1229.3)	13.6 (2.5)	5.66 (1.58)	11.26 (4.26)	−25.54 (1.11)	12.10 (1.59)

Note: $\delta^{13}C$ and $\delta^{15}N$ = stable isotopes of carbon and nitrogen, GSI = gonadosomatic index, SD = standard deviation.

Across populations and sexes combined, the length–weight relationship was $\log_{10}(\text{weight}) = -3.986 + 2.617 * \log_{10}(\text{length})$. For subspecies *L. l. lota* (i.e., Burbot from Inuvik, Aklavik, and Fort McPherson populations) the length–weight relationship was $\log_{10}(\text{weight}) = -3.882 + 2.583 * \log_{10}(\text{length})$ ($n = 311$). For subspecies *L. l. maculosa* (i.e., Burbot from the Tsiigehtchic population) the length–weight relationship was $\log_{10}(\text{weight}) = -5.458 + 3.102 * \log_{10}(\text{length})$ ($n = 27$).

Ecological variation across populations

The mean $\delta^{15}N$ in the four Burbot populations ranged from 11.33 ± 1.21 to 13.43 ± 1.32. Values of $\delta^{13}C$ ranged from −24.49 ± 0.87 to −26.03 ± 1.05 (Table 2). Populations differed significantly in stable isotope composition, for both $\delta^{13}C$ and $\delta^{15}N$ (Table 3, Figure 2). Populations from Inuvik and Fort McPherson differed most, both in $\delta^{15}N$ ($P < 0.001$) and $\delta^{13}C$ values ($P < 0.001$) (Table 3). Northern populations tended to differ significantly in their $\delta^{15}N$ isotope composition when compared to southern populations (Fort McPherson versus Aklavik: $P = 0.013$, Inuvik versus Fort McPherson: $P < 0.0001$, Tsiigehtchic versus Inuvik: $P = 0.002$) except for the populations Tsiigehtchic versus Aklavik ($P = 0.176$), although Fort McPherson versus Aklavik was not statistically significant after Bonferroni correction at $\alpha = 0.05$ ($P > 0.0083$). Comparisons of $\delta^{15}N$ isotope composition within the two northern populations (Inuvik–Aklavik) and the two southern populations (Tsiigehtchic–Fort McPherson) were not significantly different. The opposite was the case for $\delta^{13}C$ isotope composition, where most populations differed significantly, except for two comparisons between north and south populations (Fort McPherson–Aklavik and Tsiigehtchic–Inuvik, the latter not significantly after Bonferroni correction).

Stomach contents of Burbot consisted mainly of four fish species: Ninespine Stickleback (*Pungitius pungitius* [L, 1758]), Broad Whitefish (*Coregonus nasus* [Pallas, 1776]), Burbot, and Northern Pike (*Esox lucius* [L, 1758]). Aside from fish, some stomachs contained pebbles or vegetation and one fish's stomach (from Tsiigehtchic) contained a mouse; however, overall, non-fish contents were extremely rare (data not shown). The absolute number of prey items in a stomach varied quite widely (data not shown). Overall Northern Pike was the most frequent prey item (53–66%). Populations differed significantly in which prey items they had consumed ($\chi^2 = 2054.8$, df = 9, $P < 0.001$, Table 3). Tsiigehtchic differed significantly from Aklavik ($P = 0.003$) and Inuvik ($P = 0.003$) populations and from the Fort McPherson ($P = 0.028$) population, although this latter difference was not significant after Bonferroni correction (Table 3). The most prominent differences in consumed prey items between Tsiigehtchic and the other populations were that the Tsiigehtchic populations lacked Burbot, had few Ninespine Sticklebacks, and had a high proportion of Broad Whitefish (Figure 3).

TABLE 3. Statistical analyses of morphological and ecological differences between populations of Burbot subspecies (*Lota lota lota* and *L. l. maculosa*) collected from four populations in the Mackenzie River Delta, Northwest Territories, Canada, using analysis of covariance (ANCOVA) with generalized linear model and F or χ^2 tests. A. Interactions between population and age, length, weight, and trophic parameters. A significant interaction indicates that populations differed in that parameter. B. Uncorrected probability values from further population pairwise comparisons indicate which populations differed from each other in the parameters identified in A as differing significantly ($P < 0.001$).

A	Parameter	n	df	F value	P value
	Age	88	3	3.70	0.0176
	Length	338	3	10.51	< 0.001
	Weight	338	3	20.37	< 0.001
	$\delta^{15}N$	103	3	7.16	< 0.001
	$\delta^{13}C$	103	3	12.34	< 0.001
	Parameter	n	**df**	χ^2	P **value**
	Stomach contents	322	9	2054.8	< 0.001

B	Populations	Probability values: Weight	Length	$\delta^{15}N$	$\delta^{13}C$	Stomach contents
	FM-AK	0.009	0.0003**	0.013	0.864	0.109
	IN-AK	0.129	0.758	0.113	< 0.0001***	0.905
	TS-AK	< 0.0001***	0.022	0.176	0.004*	0.003*
	IN-FM	< 0.0001***	0.0009**	< 0.0001***	< 0.0001***	0.143
	TS-FM	0.031	0.14	0.217	0.0008**	0.028
	TS-IN	< 0.0001***	0.047	0.002*	0.043	0.003*

Note: df = degrees of freedom, IN = Inuvik, AK = Aklavik, FM = Fort McPherson, and TS = Tsiigehtchic.
Note: Bonferroni corrected values at α of 0.05 (* = $P < 0.0083$), 0.01 (** = $P < 0.0017$) or 0.001 (*** = $P < 0.0002$).

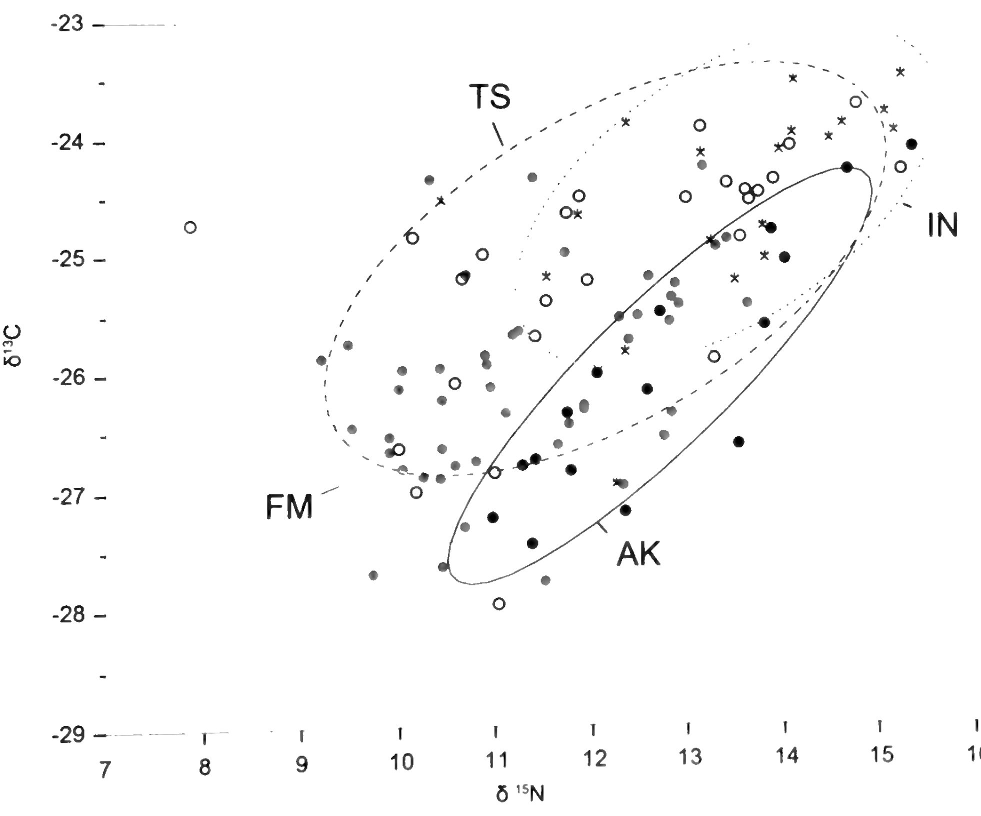

FIGURE 2. Individual carbon and nitrogen stable isotope composition of four populations of Burbot subspecies (*Lota lota lota* and *L. l. maculosa*) from the Mackenzie River Delta, Northwest Territories, Canada. Populations are circumscribed by 75% confidence ellipses: IN = Inuvik (asterisks and dotted line), AK = Aklavik (black circles and solid line), FM = Fort McPherson (grey circles and grey line), and TS = Tsiigehtchic (open circles and dashed line).

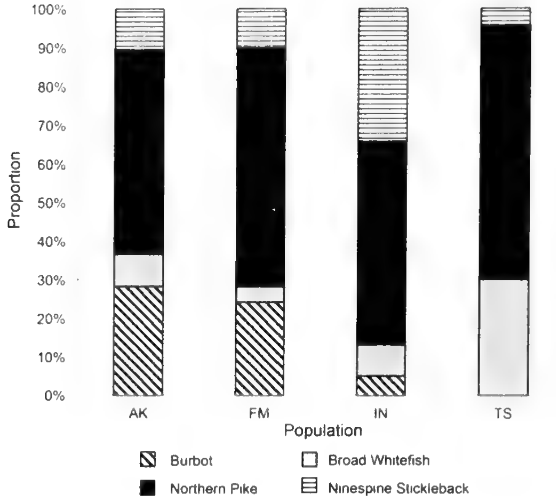

FIGURE 3. Average proportion of four main prey items found in the stomachs of four populations of Burbot subspecies (*Lota lota lota* and *L. l. maculosa*) from the Mackenzie River Delta, Northwest Territories, Canada: IN = Inuvik (n = 87), AK = Aklavik, (n = 120), FM = Fort McPherson (n = 105), and TS = Tsiigehtchic (n = 10).

Discussion

Sexual dimorphism

We found that, consistently across populations, females had greater total length and were heavier than males. In contrast, a study by Cott *et al.* (2013a) found a low level of sexual dimorphism in Burbot and no differences in body size between males and females, and, in general, it has been suggested that there is little sexual dimorphism in terms of size of Burbot. In addition, we found GSI to be significantly different between females and males (means 5.66 and 11.26, respectively). In a study spanning lakes in the *L. l. maculosa* range across Canada, Cott *et al.* (2013b) also found a higher GSI among males, with GSI in both sexes at spawning time similar to our findings. Compared with other fish species, Burbot has a relatively high value of GSI, which suggests that their reproductive behaviour includes external fertilization and high communal spawning (Stockley *et al.* 1997; Cott *et al.* 2013a). This is in agreement with observations from nature that Burbot spawn in aggregations with many males surrounding one or two females and that Burbot are broadcast spawners (McPhail and Paragamian 2000). The high GSI also indicates that sperm competition may be present in Burbot males (Stockley *et al.* 1997; Bekkevold *et al.* 2002; Cott *et al.* 2013a). Other research has suggested that GSI in Burbot can be highly variable at spawning time (Wiggs 1974); thus, this may warrant further investigation.

Morphology

Populations varied significantly in weight and length. The sampled population from Tsiigehtchic weighed less than other populations and, on average, was also smaller in total length, although the differences were not always statistically significant when controlled for age, sex, and multiple testing. Variation in Burbot morphology has been proposed to be a result of different life histories, as lotic Burbot are exposed to a different environment than lentic Burbot, and from their evolutionary history, as isolation during several cycles of glaciation has led to different genetic lineages (Fisher *et al.* 1996; McPhail and Paragamian 2000; Elmer *et al.* 2008). Therefore, the variation we found in weight and length may result from a different evolutionary history, as fish from Tsiigehtchic genetically belong to the *L. l. maculosa* lineage (Elmer *et al.* 2012) in contrast to the other populations, which belong to the *L. l. lota* lineage. Because our sampling included only one *L. l. maculosa* population, Tsiigehtchic, we cannot conclude that observed differences in length, weight, and diet were a result of ecological differences between the two subspecies rather than simply local interpopulation variation.

The weight–length relationship of Burbot in the Mackenzie River Delta had an intercept of −3.986 and a slope of +2.617 when all populations were combined. This relationship differed between *L. l. maculosa* and *L. l. lota* populations, consistent with differences found for each variable separately. Fisher *et al.* (1996) found that Burbot have a slightly different weight–length relationship, on average, across 79 populations, with an intercept of −4.868 and a slope of +2.898, and recommended only including individuals longer than 20 cm because weight measurements tend to be imprecise for small fish. All individuals in our analysis were considerably longer than 20 cm; therefore, breadth of initial sampling is not likely to explain differences between studies. Although Fisher *et al.* (1996) found considerable local variation in the Burbot weight–length relationship across its range, other research has found relatively little variation in size across lakes that differed in climate, productivity, or ecosystem size (Cott *et al.* 2013b). The extent of morphological variation may depend somewhat on environmental features, such as lentic versus lotic water bodies as well as post-glacial patterns, and deserves further research effort.

Ecological variation

Heavier isotopes are concentrated with ascent up the trophic chain, such that $\delta^{15}N$ composition is higher in carnivores than herbivores (Post 2002). We found Burbot are situated in a high trophic position as indicated by their relatively high $\delta^{15}N$. In a study conducted by Hesslein *et al.* (1991) in the Mackenzie River Delta, the highest trophic level was achieved by Northern Pike and Lake Trout (*Salvelinus namaycush* [Walbaum in Artedi, 1792]), with values of $\delta^{15}N$ of 12.3–15 in Travaillant Lake and 12–14 in Kukjuktuk Creek. Burbot were not included in that study. We found Burbot to have a mean $\delta^{15}N$ of 12.1, which is close to the level of the top predators, Lake Trout and Northern Pike, in Hesslein *et al.* (1991). A study investigating stable isotopes of Burbot and other piscivo-

rous fish from water bodies close to Great Slave Lake in Canada (approximately 1400 km upstream from the Mackenzie River Delta) found that Burbot occupy a high trophic position, similar to Lake Trout and higher than Northern Pike and Lake Whitefish (*Coregonus clupeaformis* [Mitchill, 1818]) (Cott *et al.* 2011). Variation in $\delta^{13}C$ could result from differences in abundance, interactions, and composition of organisms at lower trophic levels (primary producers and herbivores) and, therefore, provides information about the ultimate energy source of higher consumers, as the ratio changes little moving up the food chain (Zanden and Rasmussen 1999; Post 2002). Our findings place Burbot with a carbon signature similar to that found for Lake Whitefish and Broad Whitefish in previous studies (e.g., Hesslein *et al.* 1991).

The trophic niche inferred from stable isotope levels is also supported by our analysis of stomach contents, which consisted almost exclusively of fish prey. Other authors have noted that adult Burbot are piscivorous, with usually more than 80% of their diet consisting of fish and the remainder of macroinvertebrates and insects (Bailey 1972; McPhail and Paragamian 2000; Amundsen *et al.* 2003). Burbot in the Great Lakes may eat a greater variety of fish prey species (Bailey 1972; Fratt *et al.* 1997). In our study, stomach contents consisted almost entirely of fish and of only four species. Altogether, the stable isotope data and the stomach content analyses underline the piscivorous lifestyle of Burbot and their high trophic position in aquatic food webs.

Burbot populations differed significantly in $\delta^{15}N$ and $\delta^{13}C$. We found differences in $\delta^{15}N$ between populations from Fort McPherson and Inuvik and between those from Tsiigehtchic and Inuvik, but no other populations differed. In contrast all populations differed in $\delta^{13}C$ composition except for Aklavik–Fort McPherson and Tsiigehtchic–Inuvik. Values of $\delta^{15}N$ and $\delta^{13}C$ are known to differ within species between different water bodies, at least partly due to variable baselines (e.g., Cott *et al.* 2011). However, our stomach content analyses confirm that there are at least subtle differences in ecology between populations. As in morphological analyses, Tsiigehtchic was the most divergent population and significantly differed from two of the other three populations. In contrast to other populations, Burbot from Tsiigehtchic showed no cannibalism and their stomachs contained a high proportion of Lake Whitefish.

The trophic analysis indicates complex interactions between Burbot and their resources, which differ locally, leading to variation in consumed prey and the signals of stable isotopes. It is important to note that stable isotope composition reflects a long-term (weeks or months) integration of diet, whereas stomach contents are a snapshot of the day of collection and are inherently more variable. As observed in morphological analysis, Burbot caught in Tsiigehtchic were most different ecologically from Burbot caught in other locations, but it remains to be tested whether this difference is a result of local interspecific variation or fixed between subspecies.

Other research found that Burbot from Tsiigehtchic had fewer liver parasites than fish from Aklavik, Inuvik, or Fort McPherson (Goater 2010*). In other freshwater fish, parasite load has been found to be tightly correlated with trophic niche; pelagic fish have a higher parasite load, even within the same lake and the same species (Knudsen *et al.* 2013). More intensive sampling near the contact zone would be necessary to address the interesting possibility that either subspecies or localities differ in ecology or parasite susceptibility.

Implications for future research

Future research efforts should target the contact zone and its surrounding areas more intensively. Our study suggests that the Tsiigehtchic population (i.e., the only *L. l. maculosa* population) may differ in body length compared with all other sampled populations, which were *L. l. lota*. The extent to which this correlates with other morphological and ecological traits, such as trophic niche and dietary preferences, is less clear. Although we were unable to distinguish between population and subspecies differences because we sampled only one *L. l. maculosa* population, our study illuminates several lines of future research. From an ecological and morphological aspect, it would be interesting to identify the differences — if any exist — between Burbot subspecies. From a genetic perspective, previously identified low levels of admixture at the contact zone (Elmer *et al.* 2012) may provide an opportunity to hone in on the genetic basis of traits that differ between subspecies through high-resolution genomic analyses (*sensu* Buerkle and Lexer 2008). Now that the contact zone has been rather precisely located and some key parameters of variability characterized, we suggest that this geographic, ecological, and genetic suture zone would be an excellent launch pad for evolutionary and ecological research on Burbot.

Acknowledgements

This research was funded by the Gwich'in Renewable Resource Board, Aurora Research Institute, Environment Canada's Northern Ecosystem Initiative, and Fisheries and Oceans Canada (A.A.). H.R. was funded by a Leonardo da Vinci exchange to the University of Glasgow. K.R.E. thanks R. Eckmann for advice with analyses. Thanks to Marlene Evans (Environment Canada) for organizing the stable isotope analyses, and to Dr. Cameron Goater (University of Lethbridge), Dr. Terry Dick (University of Manitoba), and Nathan Millar (Yukon Government) for advice and support throughout the project. Thanks to all the Gwich'in participants who assisted with the project (sample collection, traditional knowledge, and macro stomach analysis).

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Received 11 February 2014
Accepted 28 March 2014

Observations of the Summer Birds of Tukarak Island (Belcher Islands, Nunavut), Nastapoka Islands (Nunavut), and Lac Guillaume-Delisle (Northern Quebec)

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Swarth, Christopher W., and Wouter Bleeker. 2014. Observations of the summer birds of Tukarak Island (Belcher Islands, Nunavut), Nastapoka Islands (Nunavut), and Lac Guillaume-Delisle (northern Quebec). Canadian Field-Naturalist 128(4): 385–392.

In a survey of land and water birds of Tukarak and Nastapoka Islands and Lac Guillaume-Delisle in summer 2011, we recorded 22 of the 30 species known to breed on the Belcher Islands, as well as five non-breeding species, and we observed 32 species in Lac Guillaume-Delisle. In all areas surveyed, we observed a total of 43 species: 10 waterfowl, 2 gallinaceous birds, 3 loons, 2 hawks, 3 shorebirds, 1 auk, 3 gulls, 2 falcons, and 17 songbirds. In this area of Hudson Bay, a number of species reach the southern or northern limit of their breeding distribution in eastern Canada. In light of the impact that climate change may have on bird distribution in northerly latitudes, the Belcher Islands and adjacent mainland areas could be particularly useful locations for monitoring changes in the breeding range of birds.

Key Words: Breeding birds; Hudson Bay; Belcher Islands; Tukarak Island; Lac Guillaume-Delisle; Nastapoka Islands

Introduction

The breeding avifauna of the Belcher Islands, Nunavut, has been documented by Twomey (1942), Todd (1963), Freeman (1970), and Manning (1976). Twomey was the first to make systematic bird observations on the Belcher Islands, which he described in general terms in *Needle to the North* (Twomey 1942). On Tukarak and Flaherty Islands, Twomey collected 19 bird species (273 specimens and 59 clutches of eggs); his collection is held at the Carnegie Museum of Natural History, Pittsburgh, Pennsylvania. Freeman (1970) spent the summers of 1959 and 1960, and March and April 1961 in the area. Most of his observations were made in the southwest region of Flaherty Island near the mouth of the Kasegalik River, although he also visited Tukarak Island. Manning (1976) visited the islands from May to September 1971, principally to study polar bears, but he also collected birds and estimated the size of breeding populations. More recently, information on Common Eiders was summarized by Abraham and Finney (1986) and by Robertson and Gilchrist (1998). Arctic Tern and gull population trends on the Belcher Islands were described by Gilchrist and Robertson (1999). A checklist of the bird life of Nunavut (Richards and White 2008) is based on recent sightings from throughout this vast territory. A report by the Kativik Regional Government (KRG 2007) on plans to create national parks in the western Ungava Peninsula includes a list of birds of Lac Guillaume-Delisle. The Quebec Breeding Bird Atlas (www.atlas-oiseaux.qc.ca/index_en.jsp), now in its fifth year, is mapping recent sightings by birdwatchers to Lac Guillaume-Delisle.

This report summarizes bird observations made from 17 to 30 July 2011 in eastern Hudson Bay, Canada, specifically on Tukarak Island (Belcher Island group, Nunavut), on the Nastapoka Islands (Nunavut), and in Lac Guillaume-Delisle (northern Quebec). Considering the long periods between visits by ornithologists to these remote areas, our observations augment the earlier more lengthy surveys and contribute new knowledge of the bird life of this region.

Study Area

The Belcher Islands (56°00' to 57°30'N, 79°30' to 80°00'W) comprise 1500 islands and islets covering almost 3000 km^2 in eastern Hudson Bay (Figure 1a). They are located about 120 km off the eastern shore of Hudson Bay. This region is well north of the tree line. The only trees we observed on the Belcher Islands were low-growing willows (*Salix* spp.) and Paper Birch (*Betula papyrifera* Marshall). Also, the area around the town of Umiujaq on the mainland is mostly treeless. In contrast, Lac Guillaume-Delisle (Figure 1b) has extensive groves of spruce (*Picea* spp.), willow, and Green Alder (*Alnus viridis* [Chaix] de Candolle), especially in ravines and along the lower sections of streams.

Methods

In 2011, we visited Tukarak Island in the Belcher Islands group (17–24 July), Lac Guillaume-Delisle (25–30 July), and several of the Nastapoka Islands near Umiujaq (25 and 30 July). Our primary purpose was to investigate geological formations in this region; however, each day we made a concerted effort to identify, count, and record all the birds in every area we visited.

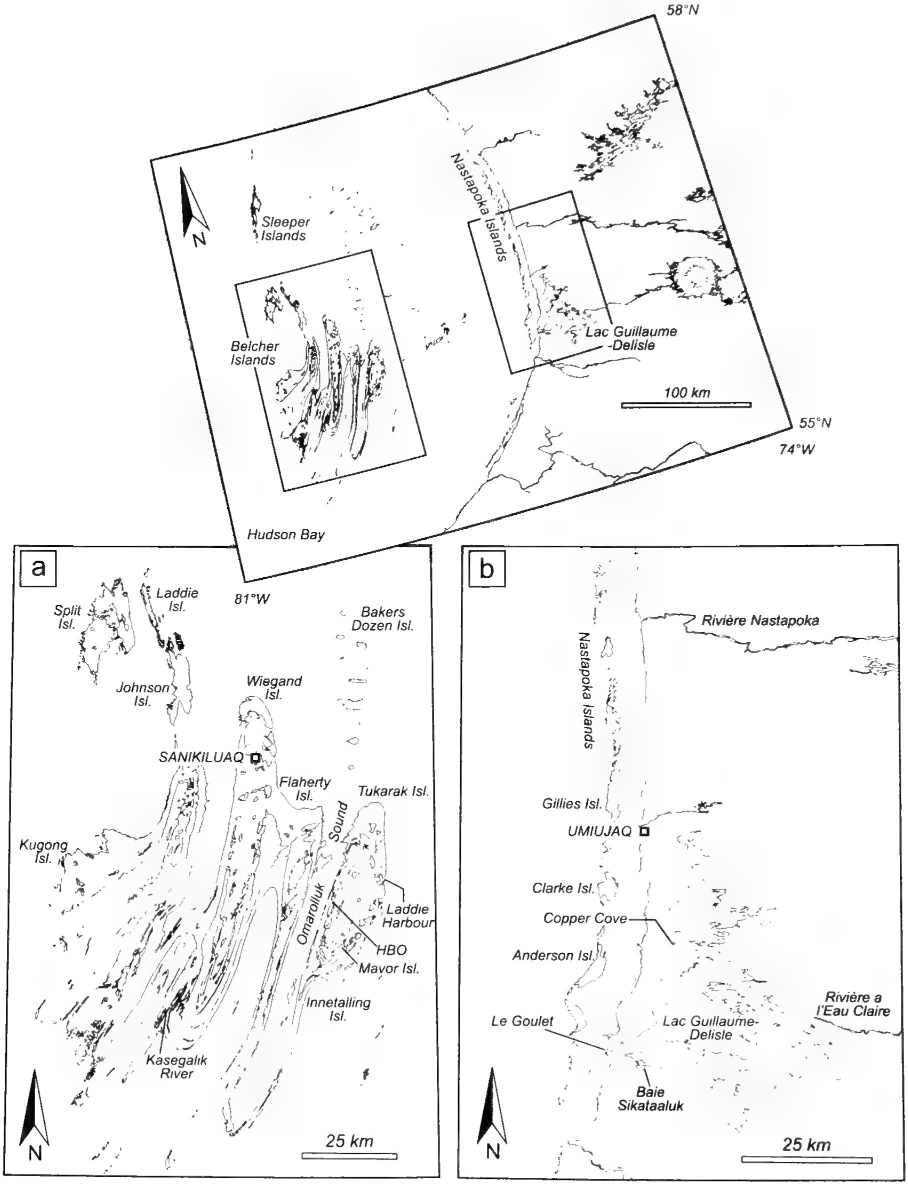

FIGURE 1. Locations of 2011 fieldwork in eastern Hudson Bay: Tukarak Island (Belcher Island group), Nunavut (a); Lac Guillaume-Delisle, Quebec; and the Nastapoka Islands, Nunavut (b). HBO = Hudson Bay outpost.

We traveled to and between the islands on the fishing boat, *Kakivak*, skippered by Inuit fishermen from Inukjuak, Quebec. While traveling across open water between shore-based sites, we maintained a constant watch and tallied all waterbirds visible from the boat. At night we anchored near shore, which provided excellent views of the rocky shorelines and beaches. Each day, we covered about 5–10 km on foot across a variety of habitats: dry and moist tundra, exposed rock formations, small streams, willow-covered ravines, and lakes, which we circumnavigated. We observed birds with 8× binoculars and a 20–60× spotting scope. The figures in the tables represent the sum total of independent daily surveys that were often, but not always, made separately by the two observers. We took care to avoid combining duplicate counts of the same birds. On the boat, the observers scanned the open waters from opposite sides of the boat. C.W.S. devoted about 12 hours each day to bird observations and W.B. about 6 hours.

Observations on Tukarak Island were concentrated in three areas: the southeast region; around the old Hudson Bay outpost along Omarolluk Sound on the west side; and at Laddie Harbour on the east-central side of the island (Figure 1a). We did not visit any of the small coastal islets.

In the Nastapoka Island group, we visited Clarke, Anderson, and Gillies Islands. In Lac Guillaume-Delisle, fieldwork took place in Baie Sikutaaluk near the Gulf ("Le Goulet"), south of the mouth of the

Rivière à l'Eau Claire, and at Copper Cove on the west-central shore (Figure 1b).

Results

On the Belcher Islands, we observed 22 of the 30 species that are regular or occasional breeders there (Table 1). Breeding species not observed were King Eider (*Somateria spectabilis*), Long-tailed Duck (*Clangula hyemalis*), Semipalmated Sandpiper (*Calidris pusilla*), Red-necked Phalarope (*Phalaropus lobatus*), Parasitic Jaeger (*Stercorarius parasiticus*), Arctic Tern (*Sterna paradisaea*), Snowy Owl (*Bubo scandiacus*), and Common Redpoll (*Carduelis flammea*). We also observed five migrant, non-breeding species. The summer avifauna of the Lac Guillaume-Delisle region, in contrast, is richer than that of the Belcher Islands. In the former, we observed 22 species that breed in this region (including Umiujaq and the Nastapoka Islands) and 10 migrants (Table 2). In all areas surveyed, we observed a total of 43 species: 10 waterfowl, 2 gallinaceous birds, 3 loons, 2 hawks, 3 shorebirds, 1 auk, 3 gulls, 2 falcons, and 17 songbirds. Several sightings represent extra-limital records of birds well north of their regular breeding range. The notes that follow summarize details about these observations.

On Tukarak Island, we observed flocks of 164 and 200 flightless Canada Geese (*Branta canadensis*), adults and goslings, and a flock of about 200 on Clarke Island (Nastapoka Island group). We observed adult Tundra Swans (*Cygnus columbianus*) swimming on lakes on Tukarak Island, but we did not see any cygnets.

We saw Common Eiders (*Somateria mollisima sedentaria*) daily in the coastal waters around Tukarak Island and in Lac Guillaume-Delisle. No eiders were seen on any inland lakes and we saw no nests. In the waters around Tukarak Island, over 90% of males were in breeding plumage, and we observed many females there with broods of various ages. The first male seen in eclipse plumage near Tukarak Island was on 21 July, whereas all the males we identified in Lac Guillaume-Delisle were in eclipse plumage.

Three male Harlequin Ducks (*Histrionicus histrionicus*) were seen at Copper Cove, Lac Guillaume-Delisle, on two days; presumably the same group was seen each day.

Scoters were seen almost daily. Of those we were able to identify to species, Surf Scoters (*Melanitta perspicillata*) were the most abundant. The largest single flock of 1200 unidentified scoters was seen on Lac Guillaume-Delisle on 27 July. Black Scoters (*M. americana*) were seen on Lac Guillaume-Delisle, but not on Hudson Bay proper. The 30 Red-breasted Mergansers (*Mergus serrator*) in Lac Guillaume-Delisle on 27 July were flightless and in a single flock.

Two female Northern Harriers (*Circus cyaneus*) were seen on Lac Guillaume-Delisle on 27 July, and one female flying with prey was in Umiujaq on 30 July.

Spotted Sandpipers (*Actitis macularius*) were seen on four days along the shores of Lac Guillaume-Delisle. An adult was attending three, one-third-grown chicks on 26 July.

Two Purple Sandpipers (*Calidris maritima*), the only ones seen during our trip, flew in and briefly mobbed us on Tukarak Island on 17 July.

Black Guillemots (*Cepphus grylle*) were observed around Tukarak Island and on Lac Guillaume-Delisle on 10 of 15 days for a mean of 27 per day. The highest daily counts were 88 near Tukarak Island and 61 on Lac Guillaume-Delisle. The guillemots were often in pairs, or in groups of 10 or fewer, and all were in breeding plumage. No birds were perched on rocks or cliffs, nor were any carrying food, and we saw no juveniles. These observations suggest that they were not nesting in these areas at this time.

Glaucous Gulls (*Larus hyperboreus*) were seen on eight days on Hudson Bay. The largest group was 10 at Laddie Harbour on 22 July, where several half-grown chicks were seen on rocks near the water's edge. No Glaucous Gulls were seen on Lac Guillaume-Delisle. Great Black-backed Gulls (*Larus marinus*) were observed on five days. An adult pair was seen at Tukarak Island on 18 July and five (four adults and one third-year bird) were seen near the Nastapoka Islands on 25 July. We saw nothing to suggest that they had nests, and we saw no chicks.

Peregrine Falcons (*Falco peregrinus*) were seen at two locations on Tukarak Island. On 19 July one flew along the cliffs at the south end of the island. On 23 and 24 July, we observed a pair closely for several hours and photographed them at their nest at Laddie Harbour. The nest site was on a sparsely vegetated ledge on a vertical cliff, 7–10 m above the water at the head of a small cove. The nest held two downy young, which appeared to be several weeks old based on their size and white downy plumage, and a single egg. At one point, the male arrived clutching an adult Horned Lark (*Eremophila alpestris*).

Single Hermit Thrushes (*Catharus guttatus*) were seen and heard singing in a wooded area along the south shore of Lac Guillaume-Delisle on 25 and 27 July.

Discussion

Many bird species currently reach the northern or southern limit of their breeding range in the eastern Hudson Bay region (Godfrey 1986), making this area especially interesting from a zoogeographic perspective. However, range boundaries are rarely static and arctic regions are changing rapidly in response to climate change (Serrize *et al.* 2000; Comiso 2003). Bird populations, especially those at high latitudes, could undergo significant range shifts in the near future (Jetz *et al.* 2007).

Few ornithologists have visited the Belcher Islands, in part because of their remote location and the associated logistics and costs that make access difficult. Lac Guillaume-Delisle is also remote, although plans to create a national park there could increase visits in

TABLE 1. Species and daily counts of birds observed on the Belcher Islands, Nunavut, in July 2011.

		Tukarak Island (east side)					Tukarak Island Laddie Harbour			
Species	Status: breeding (B) or migrant (M)	17 July	18 July	Tukarak and Mavor Islands 19 July	Tukarak Island (old Hudson Bay outpost) 20 July	Omarolluk Sound to (Laddie Harbour) 21 July	22 July	23 July	Tukarak Island (Laddie Harbour) and Umiujaq 24 July	Days observed
Canada Goose (*Branta canadensis*)	B	12		20	62	2	200		164	6
Tundra Swan (*Cygnus columbianus*)	B	3	2				4		1	4
Northern Pintail (*Anas acuta*)	B	2								1
Common Eider (*Somateria mollisima sedentaria*)	B	6	11	180	523	260	26	1		7
Surf Scoter (*Melanitta perspicillata*)	M	200		50	46	5				4
White-winged Scoter (*Melanitta fusca*)	M			6	38	25				3
Unidentified scoter (*Melanitta* sp.)	—			100	150		10			3
Common Goldeneye (*Bucephala clangula*)	M					1 (F)	1 (M)			2
Red-breasted Merganser (*Mergus serrator*)	M	1 (M)		1		21	26		17	5
Rock Ptarmigan (*Lagopus muta*)	B		1							1
Red-throated Loon (*Gavia stellata*)	B		2			2				2
Pacific Loon (*Gavia pacifica*)	B				2	2				2
Common Loon (*Gavia immer*)	B						3			1
Rough-legged Hawk (*Buteo lagopus*)	B								1	1
Semipalmated Plover (*Charadrius semipalmatus*)	B	4		2	1	2			1	5
Purple Sandpiper (*Calidris maritima*)	B	2								1
Herring Gull (*Larus argentatus*)	B	2			12	6		2	1	5
Glaucous Gull (*Larus hyperboreus*)	B	1	1	3	8	6	10	5	8	8
Great Black-backed Gull (*Larus marinus*)	M		2			1		1		3
Black Guillemot (*Cepphus grylle*)	B	20	15	6	88	11				5
Peregrine Falcon (*Falco peregrinus*)	B			1			2 (M,F)	2 (M,F)	2 (M,F)	4
Common Raven (*Corvus corax*)	B		1	2	2					3
Horned Lark (*Eremophila alpestris*)	B						3	1	3	3
American Pipit (*Anthus rubescens*)	B	1	2	1	10		20	5		6
Lapland Longspur (*Calcarius lapponicus*)	B						3			1
Snow Bunting (*Plectrophenax nivalis*)	B	1							1	2
Savannah Sparrow (*Passerculus sandwichensis*)	B				4		4			2
White-crowned Sparrow (*Zonotrichia leucophrys*)	B				5					1

Note: M = male, F = female.

TABLE 2. Species and daily counts of birds observed in Lac Guillaume-Delisle (Copper Cove, Rivière à l'Eau Claire, Baie Sikutaaluk), Quebec, and Nastapoka Islands (Umiujaq, Clark Island), Nunavut, in July 2011.

Species	Status: breeding (B) or migrant (M)	Umiujaq, Clarke Island, and Lac Guillaume-Delisle 25 July	Baie Sikutaaluk and near Rivière à l'Eau Claire 26 July	Near Rivière à l'Eau Claire and Copper Cove 27 July	Copper Cove 28 July	Copper Cove and Nastapoka Islands 29 July	Nastapoka Islands and Umiujaq 30 July	Days observed
Canada Goose (*Branta canadensis*)	B	200						1
Common Eider (*Somateria mollisima sedentaria*)	B	230	28	80		78	36	5
Harlequin Duck (*Histrionicus histrionicus*)	M			3 (M)		3		2
White-winged Scoter (*Melanitta fusca*)	M	200				4		2
Black Scoter (*Melanitta americana*)	M		60			3		2
Unidentified scoter (*Melanitta* sp.)				1200			80	2
Common Goldeneye (*Bucephala clangula*)	M					1 (F)		1
Red-breasted Merganser (*Mergus serrator*)	B	16		30		4		3
Spruce Grouse (*Falcipennis canadensis*)	B			1				1
Pacific Loon (*Gavia pacifica*)	M			1				1
Common Loon (*Gavia immer*)	B	5		2	2	1		4
Northern Harrier (*Circus cyaneus*)	M			2 (F)			1	2
Semipalmated Plover (*Charadrius semipalmatus*)	B			1				1
Spotted Sandpiper (*Actitis macularius*)	B	2	4	1		2		4
Black Guillemot (*Cepphus grylle*)	B	61	5	55		5	2	5
Herring Gull (*Larus argentatus*)	B	18	82	16	1	23	1	6
Glaucous Gull (*Larus hyperboreus*)	M	2					1	2
Great Black-backed Gull (*Larus marinus*)	M	5				1		2
Merlin (*Falco columbarius*)	B			1				1
Gray Jay (*Perisoreus canadensis*)	B			1				1
Common Raven (*Corvus corax*)	B	4					6	2
Tree Swallow (*Tachycineta bicolor*)	B	2						1
American Pipit (*Anthus rubescens*)	B	9			3	1		3
Hermit Thrush (*Catharus guttatus*)	M	1		1				2
American Robin (*Turdus migratorius*)	B			2				1
Orange-crowned Warbler (*Oreothlypis celata*)	M		1	1				2
Yellow Warbler (*Setophaga petechia*)	B				1			1
Savannah Sparrow (*Passerculus sandwichensis*)	B	8				10	6	3
Fox Sparrow (*Passerella iliaca*)	B						1	1
White-throated Sparrow (*Zonotrichia albicollis*)	B		1		2			2
White-crowned Sparrow (*Zonotrichia leucophrys*)	B	8	1		9	12		4
Dark-eyed Junco (*Junco hyemalis*)	B			12				1
Common Redpoll (*Acanthis flammea*)	B	3	2		40	1	2	5

Note: M = male, F = female.

the near future. Knowledge of the summer bird life of the Belcher Islands and Lac Guillaume-Delisle is, therefore, based on just a few reports and publications that span many decades. Twomey's observations, summarized in a popular book (Twomey 1942), provide fascinating details about the bird life, but unfortunately the results of his extensive study were not published in the scientific literature. The reports of Thomas Manning (1946, 1976) were especially thorough, and the sightings by Freeman (1970) are also useful. Based on these publications, the regular breeding avifauna is considered to consist of about 30 species. The Quebec Breeding Bird Atlas project (www.atlas-oiseaux.qc.ca/index_en.jsp) is compiling recent bird records from Lac Guillaume-Delisle, although there are few mapped sightings to date from this region. Our observational records add to the limited number of reports from eastern Hudson Bay and, especially, augment knowledge of the birds that breed or spend the summer around the Belcher Islands. Conversely, the lack of sightings of some probable breeding species such as Red-necked Phalaropes and Common Redpolls does not mean those species were not present during our visit.

We were not able to determine the age of the flightless Canada Geese in the flocks we observed on Tukarak Island and the Nastapoka Islands. Populations in late spring and summer are likely made up of both local breeders and of migrants from southern populations. Based on satellite radio telemetry, it is known that some geese that breed on the Atlantic flyway in eastern North America migrate in June to northern Quebec and the east coast of Hudson Bay (Sheaffer *et al.* 2007) where they undergo a complete annual molt.

Tundra Swans are irregular or uncommon breeders on the Belcher Islands, which are near the southern limit of their breeding range (Godfrey 1986). Freeman (1970) saw only one pair on the Belcher Islands in mid-June 1960, and he cites a report by Burwash (1927) that suggests that swans were scarce in this region by the mid-1920s. Tundra Swans were common breeders along southern Hudson Bay in the 1800s, but heavy hunting greatly reduced their numbers thereafter. Swans did not begin to re-inhabit these areas until the 1960s (Lumsden 1975).

The sighting of three male Harlequin Ducks was fortuitous, but not unexpected as they are known to nest around Lac Guillaume-Delisle and north to the Nastapoka River (Robertson and Goudie 1999; KRG 2007).

The breeding ranges of the Surf Scoter and the Black Scoter in North America are imperfectly known (Savard *et al.* 1998); however, in eastern Canada the centre of abundance of both species is the Ungava Peninsula. White-winged Scoters breed to the south and west. There are no records of scoters breeding on the Belcher Islands and we saw nothing to suggest that they might have been nesting during our visit.

The three Northern Harriers observed represent extralimital records, well north of their published breeding range (Godfrey 1986; Smith *et al* 2011). In the Lac Guillaume-Delisle region, there is at least one recent nesting record (KRG 2007) and a single "possible nesting" record in the Quebec Breeding Bird Atlas. The female we observed in Umiujaq was carrying prey, which suggests that a nest may have been nearby.

Purple Sandpipers were first documented as breeding on the Belcher Islands by Twomey (1942). In 1938, he collected 44 adults and 13 complete clutches (35 specimens and 7 clutches were from Tukarak Island). Clutch collection dates ranged from 9 June to 25 July 1938 (data courtesy of the Carnegie Museum of Natural History). Freeman (1970) discovered a nest containing four eggs on 8 July 1959 on an island in the Kasegalik River. Manning (1976) estimated that there were 4000 Purple Sandpipers on Kugong Island, the westernmost of the Belcher Islands. Freeman (1970) wrote (restated by Jehl 2004) that the Purple Sandpiper, along with the Semipalmated Plover, is "probably the commonest [breeding] shorebird" on the Belcher Islands. The fact that we saw just two birds suggests that large numbers may not breed regularly in the areas of Tukarak Island that we visited. Tukarak is a large island, and the areas we visited may not have been ideal breeding habitats for this and other shorebird species. Alternatively, the dates when we visited (mid to late July) are near the end of the breeding season for many sandpipers, and birds may have already departed the island. However, Twomey collected a full clutch on 25 July 1938, and Manning (1976) saw flocks of up to 150 Purple Sandpipers on Split Island (about 70 km to the northwest of Tukarak Island) in early August 1973, and he collected a male with four downy young there on 3 August. A thorough survey of all the Belcher Islands would be required to develop a clear understanding of their current breeding status. The Semipalmated Plover, Semipalmated Sandpiper, and Red-necked Phalarope also nest on the Belcher Islands (Todd 1963; Godfrey 1986); however, we observed only the plovers.

The single summer record for Least Sandpiper (*Calidris minutilla*) on the Belcher Islands is an observation of one nest by Twomey (1942) on Tukarak Island. Even though we did not observe any Least Sandpipers and Godfrey (1986) indicates that they do not nest on the Belcher Islands, further fieldwork could reveal that they are occasional breeders, as they are known to nest around Lac Guillaume-Delisle (Todd 1963; KRG 2007).

The sightings of adult Great Black-backed Gulls were noteworthy because known breeding colonies are quite distant: at Akimiski Strait, James Bay, 350 km south of the Belcher Islands (Eckert 2007; Dunn and Alderfer 2011) and 1400 km (by the coastline) northeast at the mouth of the Rivière aux Feuilles in Ungava Bay (Good 1998). The Belcher Islands could be colonized in the near future as nesting at Akimiski Strait was documented for the first time in 2007 (Eckert 2007). The Great Black-backed Gull is undergoing rap-

id range expansion throughout eastern North America (Good 1998).

We did not observe Arctic Terns. Arctic Tern populations declined between the 1980s and 1997 in the three northern regions (Sleeper, Split, and Laddie Islands) of the Belcher Islands (Gilchrist and Robertson 1999). Only 19 of the 431 islets in that region had nesting terns in 1997. This decline is attributed either to winter mortality or to emigration out of the Belcher Islands as a response to egging or disturbance by residents of Sanikiluaq, the only village on the islands. The tern surveys, summarized by Gilchrist and Robertson (1999), were not made on Tukarak Island, presumably because Arctic Terns are not known to nest on this island.

The nesting Peregrine Falcons we observed at Laddie Harbour belonged to the tundra subspecies, *P. f. tundrius*, based on the thin malar stripe, white upper breast, and extensive white in the auricular area. Freeman (1970) assigned the Peregrine Falcons he observed on Tukarak Island to *P. f. anatum*, although he provided no evidence to support this determination. The Nastapoka River represents a dividing line between *P. f. tundrius* on the north and *P. f. anatum* to the south (Murphy 1990).

The Hermit Thrushes seen in the Lac Guillaume-Delisle were extra-limital records, over 450 km north of the northern limit of their breeding range in southwestern Quebec (Godfrey 1986; Dellinger *et al.* 2012). Yves Aubrey (in KRG 2007) reports that they do nest in this area.

The Belcher Islands are the southernmost breeding site in North America for Snow Buntings (*Plectrophenax nivalis*), whereas the Yellow Warbler (*Setophaga petechia*) and White-throated Sparrow (*Zonotrichia albicollis*) are at the northern limits of their range at Lac Guillaume-Delisle. Sightings of these three species in the regions we visited are consistent with their known occurrence in eastern Canada.

In summary, the Belcher Islands are large, we only visited parts of Tukarak Island, and our fieldwork was brief — factors that make our survey less than complete. Clearly fieldwork in more areas and for longer periods is required to determine the current status of all breeding and summering birds there. The strategic location of the Belcher Islands and Lac Guillaume-Delisle — at the tree line and in a climatic zone where arctic conditions exist, as well as the fact that they support a number of species at the limits of their geographic range — make them useful sites for studying shifts in species' breeding ranges that could result from global climate change.

Acknowledgements

Our expedition was made possible by grants to Dominic Papineau and Marilyn Fogel from the Carnegie Institution of Canada, the National Aeronautical and Space Administration Astrobiology Institute, the W. M. Keck Foundation, and the Geophysical Laboratory of the Carnegie Institution of Washington. The authors and scientific team thank the municipality of Umiujaq, the Sakkuq Landholding Corporation, the Makivik Corporation, the Nunavut Research Institute, the Government of Nunavut (Department of Culture, Language, Elders and Youth), and the Qikiqtani Inuit Association for permission to conduct fieldwork on their territory. We are grateful to the captain and crew of the *Kakivak* for expert seamanship and, especially, to Arthur Elijassiapik for cheerful assistance in the field. Stephen Rogers, bird collection manager at the Carnegie Museum of Natural History, provided data on bird and egg specimens from the 1938 Twomey expedition. Jason Chartrand (GSC, Ottawa) provided GIS assistance in drafting Figure 1. David Shuford, Dominic Papineau and two anonymous reviewers made constructive comments on an early draft.

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Received 15 March 2014
Accepted 1 May 2014

Comparing the Diet of Great Horned Owls (*Bubo virginianus*) in Rural and Urban Areas of Southwestern British Columbia

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Hindmarch, Sofi, and John E. Elliott. 2014. Comparing the diet of Great Horned Owls (*Bubo virginianus*) in rural and urban areas of southwestern British Columbia. Canadian Field-Naturalist 128(4): 393–399.

We investigated the diet of Great Horned Owls (*Bubo virginianus*) in southwestern British Columbia. Our objective was to compare the diets of owls in urban and rural areas and determine whether urban owls consume a higher proportion of commensal rodents to understand possible pathways of secondary rodenticide poisoning of Great Horned Owls. Among 546 prey items identified at seven sites, Townsend's Vole (*Microtus townsendii* [Bachman, 1839]) and rats (*Rattus* G. Fischer, 1803) were the two main prey items, making up 65.9% and 13.1% of the diet, respectively. The proportion of rats in the diet was positively correlated with the degree of urban development in the owls' home range ($r_p = 0.83$, $P < 0.05$, df = 5).

Key Words: Great Horned Owl; *Bubo virginianus*; diet; British Columbia; voles; Townsend's Vole; *Microtus townsendii*; rats; *Rattus*; rodenticide

Introduction

The Great Horned Owl (*Bubo virginianus*) is found throughout North America, except in the Arctic, making it the most common and widespread owl on the continent (Houston *et al.* 1998*). The large and diverse range of the Great Horned Owl is also reflected in its diet. As a generalist and opportunistic feeder, it consumes a wide range of prey species, including lagomorphs, rodents, waterfowl, game birds, raptors, insects, and even larger birds, such as herons (Houston *et al.* 1998*; Johnsgard 2002). Although a diverse array of prey species have been identified, over most of the Great Horned Owl's range, its diet consists of 90% mammals, predominantly rodents, and 10% birds (Houston *et al.* 1998*; Johnsgard 2002).

Despite several studies and reviews investigating the food habits of the Great Horned Owl in a variety of regions of North America (Houston *et al.* 1998*; Johnsgard 2001), no Great Horned Owl diet studies have been conducted in southwestern British Columbia, and only one such study has been reported from the province (Van Damme 2005). Most previous studies have been conducted in forest, grassland, and agricultural settings; few have investigated the diet of the Great Horned Owl in more urban landscapes. Like other predatory birds, such as the Sharp-shinned Hawk (*Accipiter striatus*) and the Northern Goshawk (*Accipiter gentilis*), Great Horned Owls are increasingly finding niches in urban ecosystems across North America (Lambert 1981; Powers 1996; Rutz 2008) where their exposure to environmental contaminants may be enhanced, especially through consuming rodents that have previously ingested anticoagulant rodenticides. The risk of secondary exposure to these rodenticides in raptors is currently receiving increased attention in Canada (Albert *et al.* 2010; Thomas *et al.* 2011; Elliott *et al.* 2014).

Our study had two objectives: to obtain dietary information for Great Horned Owls in a region where no previous data had been collected and to compare the diet of owls that inhabit agricultural versus suburban landscapes in southwestern British Columbia. Such data are of particular interest in rapidly urbanizing regions, such as southwestern British Columbia, where the loss of forests and agricultural lands surrounding urban centres forces owls and other wildlife into the remaining patches of green space, such as parks, suburban woodlots, and fragments of undeveloped land. We were specifically interested in evaluating whether the amount of urban development within Great Horned Owl home ranges influenced the consumption of commensal rodents such as Norway Rats (*Rattus norvegicus* [Berkenhout 1769]), Black Rats (*Rattus rattus* [L., 1758]), and House Mice (*Mus musculus* L., 1758), which are the species commonly targeted for control with anticoagulant rodenticides.

Study Area

Surveys for Great Horned Owl nest and roost sites were conducted from December 2010 to December 2013 in the municipalities of Richmond, Vancouver, Burnaby, Delta, Surrey, and New Westminster (a total area of 847 km^2) in southwestern British Columbia, Canada (49°8'N, 122°18'W). The area includes some of the main stopover sites for birds migrating on the Pacific flyway and encompasses important wildlife areas such as the Alaksen National Wildlife Area, Burns Bog, Stanley Park, Pacific Spirit Regional Park and Boundary Bay Regional Park. Before European settlement, the low-lying floodplains were dominated by grassland, low shrub vegetation, and extensive stands of

mixed woodlands dominated by cottonwood, alder, and cedar, while higher elevations were covered primarily by mixed coniferous forest (North and Teversham 1984). Today, the landscape ranges from agricultural to suburban to highly urban, and the remaining lower grassland and forested habitats face ongoing development pressure as the projected human population in the region is expected to increase from the current 2.4 million to 3.4 million in 2040 (Metro Vancouver 2009*).

Methods

Owl surveys, pellet collection and analyses

Suitable areas to survey for nest and roost sites and, thus, pellet and prey remains were identified with the collaboration of local natural history clubs and by surveying parks and green spaces for signs of owl presence, such as whitewash, feathers, and pellets. To confirm the presence of Great Horned Owls and to guide pellet searching in larger parks, call play-back was used at dusk following the North American nocturnal owl survey guidelines (Takats *et al.* 2001*). When we found evidence of an owl roosting or nesting, we revisited the site every 2–3 months to search for additional pellets and prey remains. Although the potential for occasional loss of larger prey remains to scavenging existed (Marti *et al.* 2007), we believe there would likely be sufficient remains of such large prey items to allow identification. Incidental observations of foraging and prey type were also recorded.

Pellet analysis

We dissected pellets carefully to ensure that prey items could be identified from bone remnants, fur and other body parts using British Columbia small mammal field guides (Nagorsen 1996, 2005). We determined the number of individuals of any species in each pellet by pairing each skull with the correct number of ischia, left and right mandibles, and tibiae/fibulae or, in the case of birds, each skull with sternum, gizzard sac, and feet. We assembled the remaining bones in the pellet to determine the minimum number of additional individuals whose skull may have been crushed. For smaller prey items (< 100 g), we assumed that the remains of each were contained in a single pellet, as finding bones from one prey item in two successive pellets is rare (Raczynski and Ruprecht 1974). We estimated the weights of rats from intact jaw bones in the prey remains following Morris (1973).

Very few rat (Norway Rat or Black Rat) and shrew (Vagrant Shrew (*Sorex vagrans*) and Montane shrew (*Sorex monticolus*) prey remains were sufficiently intact to determine species) and, hence, we pooled all rats and shrews into one category. For the same reason, we allocated songbird (Passeriformes) prey remains to two categories: small songbirds (< 30 g) and medium songbirds (30–80 g). We considered all insect exoskeleton remains to belong to the order Coleoptera.

Evaluation of land use within home ranges

In examining differences in the diet of Great Horned Owls between agricultural and suburban sites, we quantified the amount of urban land (residential, industrial, and transportation) within a 1-km radius (3 km² or 300 ha) of each nest or roost site from digitized data layers using geographic information system software (ArcMap 10, Esri, Redlands, California, USA). We used a 1-km radius, as the average home range of the Great Horned Owl is approximately 3 km² (Petersen 1979*; Houston *et al.* 1998*). Data on land use within the home ranges were obtained from a 2006 Vancouver Regional District land-use layer map that categorized land parcels based on zoning (Metro Vancouver 2008*). We compared the 2006 land-use layer map with 2010 Bing Ortho photos (Bing Maps, Microsoft, Redmond, Washington, USA) to control for any recent changes in land use or discrepancies between current land use and zoning.

We conducted a Pearson correlation analysis to determine if there was any relationship between the amount of urban development within home ranges and the proportion of rats in the diet of Great Horned Owls. The Pearson correlation analysis was carried out using IBM SPSS 22 (IBM Inc. Armonk, New York, USA).

Results

We found seven sites (five nests and two roosts) occupied by Great Horned Owls in our study area and monitored them regularly. Three sites were located in predominantly agricultural landscapes (Alaksen National Wildlife Area, Forest Richmond, and Arthur Drive) and four in urban parks and green spaces (Terra Nova Park, Beach Grove Park, Crescent Park, and Central Surrey). The proportion of urban development within Great Horned Owl home ranges (3 km²) varied considerably, from 0%–7.6% at rural sites to 33.8–93.3% at urban ones (Table 1).

Pellets and prey remains were found predominantly under nest or roost trees. Some pellets were weathered considerably, and it was impossible to get an exact count of the number of pellets collected, but, in total, 546 prey items of 21 species were identified. Overall, Townsend's Vole (*Microtus townsendii* [Bachman, 1839]) was the most common (65.9%), and was the dominant prey species at six of the seven sites, followed by *Rattus* spp. (13.1%). Other species were only marginally represented in the diet, each contributing less than 5% of the total number of individuals overall (Table 1). On average 7.1 prey species were identified at each site (range 2–9), and the intact prey ranged in weight from about 1 g (e.g., beetle) to over 2 kg (Great Blue Heron, *Ardea herodias*).

In the late summer and fall of 2012, one Great Horned Owl pair residing in Terra Nova Park, Richmond, was observed by park employees preying on Barn Owls (*Tyto alba*) (Figure 1). In total, eight Barn

TABLE 1. The proportion of each prey species or taxon found in Great Horned Owl (*Bubo virginianus*) pellets and prey remains collected from December 2010 to December 2013 at seven sites ranging from 0% to 93.3% urban development in southwestern British Columbia, Canada.

Prey species	Percentage (no.) of prey at each nest or roost site							Average, % ± SD
	Alaksen National Wildlife Area	Forest Richmond	Arthur Drive	Terra Nova Park	Beach Groove Park	Crescent Park	Central Surrey	
Total prey items	99	116	81	74	51	50	75	77 ± 23
% urban development	0	7.0	7.6	33.8	38.3	61.0	93.3	34.4 ± 31.3
Order Rodentia								
Townsend's Vole (*Microtus townsendii* [Bachman, 1839])	84.8 (84)	69.0 (80)	97.5 (79)	70.3 (52)	37.3 (19)	2.1 (1)	57.3 (43)	59.8 ± 29.5
North American Deer Mouse (*Peromyscus maniculatus* [Wagner, 1845])	—	11.2 (13)	—	1.4 (1)	—	21.3 (10)	—	4.8 ± 7.7
Pacific Jumping Mouse (*Zapus trinotatus* Rhoads, 1895)	—	—	—	—	—	—	1.3 (1)	0.2 ± 0.5
Common Muskrat (*Ondatra zibethicus* [L., 1766])	1.0 (1)	—	—	—	—	—	—	0.2 ± 0.5
Rat species (*Rattus* G. Fischer, 1803)	1.0 (1)	7.8 (9)	2.5 (2)	1.4 (1)	25.5 (13)	42.6 (20)	33.4 (25)	16.2 ± 15.8
House Mouse (*Mus musculus* L., 1766)	—	0.9 (1)	—	—	—	—	—	0.1 ± 0.3
Eastern Gray Squirrel (*Sciurus carolinensis* Gmelin, 1788)	—	—	—	—	—	2.1 (1)	—	0.4 ± 1.0
Order Lagomorpha								
Eastern Cottontail (*Sylvilagus floridanus* [J.A. Allen, 1890])	—	—	—	—	23.5 (12)	4.3 (2)	2.7 (2)	4.4 ± 8.0
Order Soricomorpha								
Coast Mole (*Scapanus orarius* True, 1896)	—	—	—	—	5.9 (3)	—	—	0.8 ± 2.1
Shrew-mole (*Neurotrichus gibbsii* [Baird, 1858])	—	1.7 (2)	—	—	—	—	—	0.2 ± 0.6
Shrew species (*Sorex* spp.)	—	7.8 (7)	—	9.5 (4)	—	—	—	2.5 ± 3.9
Order Passeriformes								
Medium songbirds (*Passeriformes*; 30–80 g)*	5.1 (5)	—	—	—	2.0 (1)	10.6 (5)	1.3 (1)	2.7 ± 3.6
Small songbirds (*Passeriformes*; ≤ 30 g)*	—	0.9 (1)	—	—	2.0 (1)	6.4 (3)	—	1.3 ± 2.2
American Crow (*Corvus brachyrhynchos*)	—	0.9 (1)	—	2.7 (2)	2.0 (1)	4.3 (2)	1.3 (1)	1.6 ± 1.4
Order Anseriformes								
Family Anatidae	5.1 (5)	—	—	—	2.0 (1)	—	1.3 (1)	1.2 ± 1.7
Order Pelecaniformes								
Great Blue Heron (*Ardea herodias*)	—	—	—	1.4 (1)	—	—	—	0.2 ± 0.5
Order Strigiformes								
Barn Owl (*Tyto alba*)	—	—	—	10.8 (8)	—	—	—	1.5 ± 3.8
Order Coleoptera	3.0 (3)	—	—	2.7 (2)	—	6.4 (3)	1.3 (1)	1.9 ± 2.2

Note: SD = standard deviation.
* Unidentified songbirds were sorted into two categories based on their mass.

FIGURE 1. Great Horned Owl (*Bubo virginianus*) sitting on shed roof with a captured Barn Owl (*Tyto alba*). The Great Horned Owl pair at Terra Nova Park, Richmond, caught a total of eight Barn Owls in fall 2012. Photographed 10 October 2012 at Terra Nova Park Richmond; photo by Sharing Farm.

Owls were preyed on, most probably young of the year as band recovery confirmed that two were recently fledged chicks from nest sites 14 and 34 km away. Eastern Cottontails (*Sylvilagus floridanus* [J. A. Allen, 1890]) were not an important component of the diet and were recorded at only three urban sites. However, at one nest site located in a park, they were the second most consumed prey along with rats at 23.5%. Further, only one House Mouse (*Mus musculus* L., 1766) and one Eastern Gray Squirrel (*Sciurus carolinensis* Gmelin, 1788) were found among all prey remains.

Following Morris' (1973) model for predicting the body weight of rat prey items, the average mass of rats consumed by Great Horned Owls was 118 ± 63.3 g (range 20–280 g, $n = 39$). Based on the mode (Figure 2), Great Horned Owls most frequently consumed rats

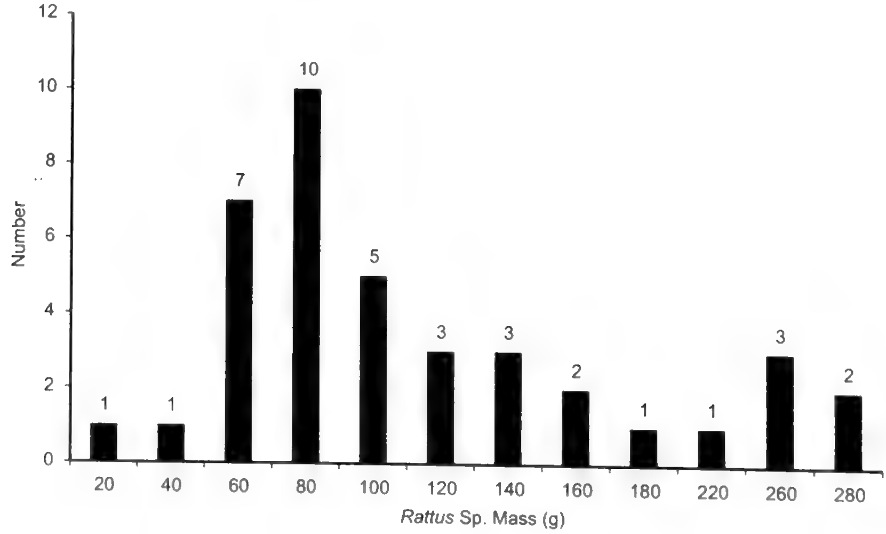

FIGURE 2. Number of rats (*Rattus* spp.) by weight class consumed by Great Horned Owls (*Bubo virginianus*) at seven sites in southwestern British Columbia, Canada (average = 118 ± 63.3 g).

weighing 80 g. The difference between the average and the mode is explained by the Great Horned Owls' capability of capturing rats of all sizes, including the occasional larger rat (> 200 g). The proportion of rats in the diet was significantly correlated with the amount of urban land within home ranges (r_p = 0.83, $P < 0.05$, df = 5).

Discussion

Despite the highly flexible foraging behaviour of Great Horned Owls, they tend to focus on only one or two profitable prey species within a geographic region (Houston *et al.* 1998*; Marchesi *et al.* 2002). The food habits of the Great Horned Owls within our study area showed no exception to this trend. Overall, Townsend's Voles dominated the diet followed by rats, and a diverse range of other species each accounted for less than 5% of the prey consumed at all sites combined. Land use surrounding individual nest and roost sites likely influenced the diversity and abundance of available prey species and, ultimately, the diet of Great Horned Owl pairs. This was evident from the consumption of rats, which increased as home ranges became gradually more urban.

The move toward increased rat consumption in more urban environments was previously documented in Great Horned Owls nesting in city parks in Seattle, Washington (Lambert 1981). Similarly, the larger cousin of the Great Horned Owl, the Eurasian Eagle Owl (*Bubo bubo*) consumed more rats when nesting in European urbanized landscapes (Marchesi *et al.* 2002; Sandor and Ionesco 2009), while the diet of a pair of Desert Eagle Owls (*Bubo ascalaphus*) in the city of Hurghada, Egypt, was made up of 71.8% House Mice and Norway Rats (Sandor and Moldovan 2010). In South Korea, Eurasian Eagle Owls consumed rats predominantly in both urban and agricultural landscapes (Shin *et al.* 2013). In all cases, the increased consumption of rats was attributed to their status as an abundant, stable, year-round food source. In our study, Great Horned Owls consumed predominantly smaller rats, which are likely to be more abundant, less risky to handle, and faster to process than larger rats.

Among other commensal rodents, only one House Mouse was found. Similarly, only one Eastern Gray Squirrel was recorded, at a nest in an urban park, despite the abundance of squirrels in all urban and rural parks, at least partly a result of public feeding (S. Hindmarch personal observation).

Second-generation anticoagulant rodenticides (SGARs) used to suppress commensal rodent populations worldwide, have been shown to be persistent, highly bioaccumulative, and very toxic to non-target species (Parmar *et al.* 1987; US EPA 2004*). Among raptors, Great Horned Owls have one of the highest rates of exposure to, and toxicity from these rodenticides (Stone *et al.* 1999; 2003; Albert *et al.* 2010; Murray 2011, Thomas *et al.* 2011). Further, predators may be at a greater risk of SGAR exposure in urban settings where larger quantities of these compounds are used to suppress commensal rodent populations (Stone *et al.* 1999, 2003; Riley *et al.* 2007; McMillin *et al.* 2008).

In southwestern British Columbia, 70% (n = 61) of Great Horned Owl carcasses tested between 1988 and 2003 contained one or more SGARs (Albert *et al.* 2010). More recently, all of the Great Horned Owls collected in southwestern British Columbia between 2005 and 2011 (n = 29) tested positive for one or more SGARs (J.E.E. unpublished data). There is some evidence to suggest that non-target species including native mice and voles, squirrels, and passerines enter SGAR bait stations and feed (US EPA 2004*; Brakes and Smith 2005; Tosh *et al.* 2012), although rats are likely one of the main vectors responsible for secondary exposure of non-target predators (Cox and Smith 1990; Birks 1998; Elliott *et al.* 2014). Our data showing increased consumption of rats by urban Great Horned Owls are consistent with the idea that rats are the main source of exposure to SGARs. However, the dominance of Townsend's Voles in the diet of Great Horned Owls suggests the need for SGAR residue sampling in non-target small mammals in addition to rats in urban environments.

Our land-use analysis may not have been able to identify fine-scale landscape differences between sites. For example, one Great Horned Owl pair nesting in an urban nature park (26 ha) consumed predominantly Townsend's Voles (70.3%), and only 2 rats were found in the pellets. Although that park is surrounded by residential development, over recent years an old field restoration project has resulted in the removal of invasive plant species and an increase in the abundance of Townsend's Voles, with the expressed goal of encouraging the nesting of raptors. This was also the site where the Great Horned Owl pair consumed eight Barn Owls and one Great Blue Heron in the fall of 2012. Great Horned Owl predation on Barn Owls has been documented previously (Rudolph 1978, Knight and Jackman 1984, Millsap and Millsap 1987, and Van Damme 2005). In this case, on several occasions we observed a Great Horned Owl entering a Barn Owl nest box to feed. Such behaviour can be prevented by reducing the size of the entry hole on Barn Owl nest boxes and installing a vertical predator guard on the inside. The size of the entry hole was reduced on all the boxes in the park shortly after these observations were made.

Our diet data revealed that Great Horned Owls in southwestern British Columbia feed primarily on voles and rats. Despite our small sample size, the consumption of rats was significantly higher among Great Horned Owls with a higher proportion of urban land within their home range. The increased consumption of rats and the negligible number of House Mice and squirrels in the diet indicate that rats could be a major

pathway for secondary SGAR exposure in Great Horned Owls.

Acknowledgements

We thank Paul Levesque and Alexa and Jamie Coote for their great help in looking for owl pellets. In many instances, their efforts included crawling around in the rough understory of urban parks. We appreciate and thank Sean McCann's efforts in proofreading and providing constructive comments on an earlier draft of this manuscript. Also, we wish to thank the two independent reviewers for their knowledgeable insights and efforts in reviewing our manuscript. Funding for this research was provided to John Elliott by the Pesticide Science Fund of Environment Canada.

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Received 17 March 2014
Accepted 28 June 2014

Grouseberry (*Vaccinium scoparium* Leiberg ex Coville) Fruit Production in Forest Openings in Banff National Park, Alberta

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Pengelly, Ian, and David Hamer. 2014. Grouseberry (*Vaccinium scoparium* Leiberg ex Coville) fruit production in forest openings in Banff National Park, Alberta. Canadian Field-Naturalist 128(4): 400–407.

Grouseberry (*Vaccinium scoparium* Leiberg ex Coville) is an abundant dwarf shrub in the understory of many areas of subalpine forest in Banff National Park and has the potential to produce fruit important for wildlife. However, the suppression and prevention of wildfires, which began in the early 1900s in the park, have reduced fire-dependent shrubland and open forest and increased the extent of closed, mature forest. Because canopy closure is typically associated with decreased fruit production by understory shrubs, the decline in fire disturbance may be reducing Grouseberry fruit production. To quantify this effect, we measured Grouseberry fruit production under various forest canopies at 10 sites in Banff during 2004–2012. We measured site openness by modeling photosynthetically active direct solar radiation (dPAR) adjusted for overshadowing by topography and coniferous foliage. We found a positive relation between Grouseberry fruit production and dPAR in 2006 and 2010–2012, but not in 2008 or 2009, the 2 years of lowest fruit production; data were lacking for 2004, 2005, and 2007. We also recorded high Grouseberry fruit densities beginning 5 years after fire removed the forest canopy in four prescribed burns conducted during 2001: fruit production was 3.3 to more than 20 times that in adjacent mature forests in 5 of the 6 years analyzed. This study shows the potential ecological benefits of both prescribed burns and wildfire in upper subalpine forests where Grouseberry is widespread, but fruit production is low under the forest canopy.

Key Words: Banff National Park; fruit production; Grouseberry; prescribed burn; photosynthetically active radiation; solar radiation; *Vaccinium scoparium*; wildfire

Introduction

Grouseberry (*Vaccinium scoparium* Leiberg ex Coville) is a dwarf shrub 10–30 cm in height that produces a small, reddish fruit 4–6 mm in diameter (Szczawinski 1962). These fruits are eaten by a variety of birds and mammals (Hamer and Herrero 1987; De Franceschi and Boag 1991; Mattson 1997). Grouseberry is abundant in the understory of many forest communities of Banff National Park, where Grouseberry forest community types cover 28% of a 123-km^2 mapped area in the Front Ranges (Hamer 1985).

Fruit production in many *Vaccinium* species is reduced, sometimes dramatically, under a forest canopy (Hamer and Herrero 1987; Noyce and Coy 1990; Jordano 2000; Greenberg *et al.* 2007). Interception of solar radiation by the forest canopy decreases the amount of photosynthetic energy available to understory plants for production of seed and fruit (Kudo *et al.* 2005). Martin (1983) recorded the production of less than 134 L/ha of Mountain Huckleberry (*V. membranaceum* Douglas ex Torrey) fruit in Montana where canopy cover was greater than 30%; in more open sites, up to 1400 L/ha of fruit were noted. Weaver *et al.* (1990) also found that the abundance of Huckleberry fruit had a strong negative relation to canopy cover (r^2 = 0.96). The importance of light was inferred in a Huckleberry study in northwest British Columbia, where fruit production was roughly 50% less in transects where the forest canopy blocked more than 40% of incoming solar radiation compared to transects in sites with greater solar radiation (Burton 1998*).

Before the 20th century, fire was the dominant ecological process affecting forests in Banff National Park. However, since the early 1900s, the incidence of wildfires has declined to a small fraction of the previous rate because of fire prevention and suppression (White 1985). We hypothesized that without wildfires, the extent of post-fire shrubland and open-canopy forest is reduced, causing a decline in Grouseberry fruit production. During 2004–2012, we studied the relation between site openness and Grouseberry fruit production in Banff National Park.

Study Area

Our study area was in the upper subalpine zone of Banff National Park (Figure 1). Annual precipitation was estimated at 50–125 cm (Janz and Storr 1977*). Warm, drying Chinook winds descend the east slopes of the Rocky Mountains and reduce moisture and snow pack, particularly on slopes with a south or west aspect.

Elevations in the park range from 1330 to 3610 m with the treeline at roughly 2300 m. The subalpine zone is at approximately 1500–2350 m. The upper subalpine area, which is generally cooler and wetter, with deeper and longer-lasting snow, begins at roughly 2000 m (Achuff 1982*). Our study sites were at an elevation of 2080–2380 m in the upper subalpine zone where Grouseberry is abundant.

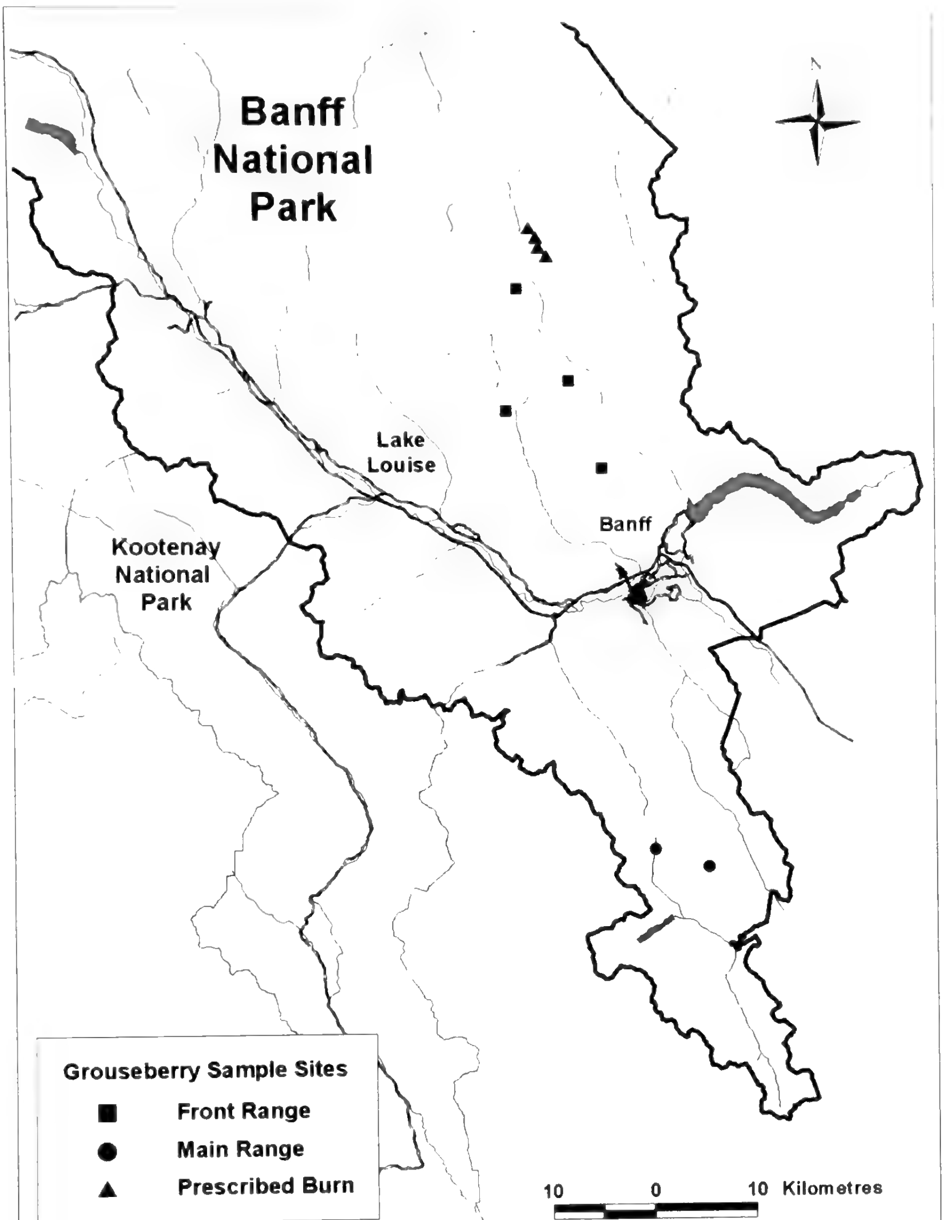

FIGURE 1. Location of Grouseberry study sites in Banff National Park, Alberta, 2004-2012.

The forests in our study area were dominated by Engelmann Spruce (*Picea engelmannii* Parry ex Engelmann). In some sites, Lodgepole Pine (*Pinus contorta* Douglas ex Loudon), Subalpine Fir (*Abies lasiocarpa* [Hooker] Nuttall), and Subalpine Larch (*Larix lyallii* Parlatore) were also abundant. The upper subalpine forest is opened by a variety of factors including fire, avalanches, semi-xeric conditions on exposed southwest-facing slopes, which can lead to grassland and shrubland, and cold air pooling in depressions at the toe of slopes (Hamer 1996).

Because of our sampling design, the understory of most sites was dominated by Grouseberry. Other frequent understory species included Heart-leaved Arnica (*Arnica cordifolia* Hooker), Fireweed (*Epilobium angustifolium* L.), Bracted Lousewort (*Pedicularis bracteosa* Bentham), Pink Mountain Heather (*Phyllodoce empetriformis* [Smith] D. Don), Arctic Willow (*Salix arctica* Pallas), Low Blueberry (*Vaccinium myrtillus* L.), Sitka Valerian (*Valeriana sitchensis* Bongard), and grasses. Regenerating Engelmann Spruce and Subalpine Fir were frequent tall shrubs; willows (*Salix* spp.) occurred in fewer than 10% of the transects.

Methods

Site selection

We established 10 study sites in total: eight in the Front Ranges and two in the Main Ranges (Figure 1). We located one Front Range site in an 1889 burn and a Main Range site in a 1920 burn. These large wildfires had burned into the upper subalpine and created shrubland and regenerating forest with varying degrees of canopy closure, including communities where Grouseberry was a dominant shrub (Hamer and Herrero 1987). Four sites were 6–10 km from the 1889 and 1920 burn sites, where we found relatively accessible terrain, communities with Grouseberry dominant in the shrub layer, and forest openings in stands originating from wildfires that had occurred between 1850 and 1900. Another four sites were located where prescribed burns had been conducted from mid-September through mid-October 2001. These fires removed the forest canopy and scorched the ground layer; *Vaccinium* shrubs had subsequently resprouted from underground rootstocks. The forests in this area were multi-aged, originating from fires that occurred from about 1800 to 1868 (Hamer and Herrero 1987).

Transect selection

We established 11 pairs of transects in the four prescribed burn sites and adjacent forests. Because the fires had run upslope from ignition points, we were able to establish pairs of burned and unburned transects where ignition, rather than habitat characteristics, was responsible for which areas burned.

Transects in the burned areas were at 60–125 m intervals (mean 90 m). Because *Vaccinium* cover was patchy following fire, we adjusted the transect locations by up to a few tens of metres from the systematically located points to ensure relatively high *Vaccinium* cover (mean 41%, standard deviation [SD] 18%). We located control transects in the unburned adjacent forest along the same elevational contour as the burned transects, with similar adjustment to locate transects in communities where *Vaccinium* was dominant in the shrub layer (mean 62%, SD 16%). We established five transect pairs in the largest burn, two pairs in a burn 1.2 km north, and two pairs in a burn 1.1 km south of the largest burn, all on westerly slopes of 215–271°. Two pairs of transects were located in a fourth burn, on an easterly slope of 84–124°.

The six additional sites in the study area were also established where *Vaccinium* was dominant in the shrub layer (mean cover 57%, SD 15%). At each site, we located one or more transects under a forest canopy cover of less than 40%. When the terrain and Grouseberry cover were suitable, we established transects with notably different slope aspects and forest cover.

Transect analysis

The ends of each transect were marked with permanent metal bars. We recorded transect location and elevation using a handheld geographic positioning system unit and slope steepness and aspect using a compass with built-in clinometer. In the year when transects were established, we estimated *Vaccinium* cover and height at 1-m intervals on the 20-m transects (i.e., 20 measurements/transect). We estimated cover visually to the nearest 5% using a 10 cm by 10 cm frame and measured height as the length of the longest *Vaccinium* shoot rooted within 5 cm of the *Vaccinium* stem rooted nearest to a preselected corner of the frame.

We estimated Grouseberry fruit density by counting all fruits within a 20 cm by 20 cm frame placed at 2–m intervals along the 20–m transect (10 quadrats/transect). At each 2–m point, a 180° forward-facing selection zone (Hamer 1996) was scanned and the frame was placed in the first available location with more than 70% *Vaccinium* cover (lower cover was accepted if the alternative meant moving the frame more than 2 m from the original 2-m point). Because of these subjective criteria, quadrats were not in exactly the same location each year. Fruits were picked to ensure that each was counted only once. *Vaccinium* cover in the quadrat was estimated to the nearest 5%. Counts were then scaled to 100% *Vaccinium* cover (e.g., a quadrat with 35 fruits and 50% *Vaccinium* cover scored 70 fruits) to allow comparison among locations with varying *Vaccinium* cover. In other words, we calculated fruits/m^2 of *Vaccinium* shrub cover, not fruits/m^2 of habitat. Because fewer than 1% of the fruits we counted in 2004–2012 were Low Blueberry, we refer to fruits as Grouseberry. Because Grouseberry and Low Blueberry can be difficult to separate based on vegetative characteristics (Szczawinski 1962, Vander Kloet and Dickinson 1999), we report cover and height for *Vaccinium* species.

Estimating solar radiation

Although forest canopy is a primary cause of shading, nearby or tall mountains also block solar radiation. Thus, we measured site openness by modeling direct photosynthetically active radiation (dPAR) adjusted for overshadowing by both topography and coniferous canopy.

We calculated the relative amount of dPAR (band 1, wavelength 290–700 nm) received at our transects under cloudless conditions by applying the REST2 model (Gueymard 2008; Gueymard and Myers 2008), using site-specific latitude, slope aspect, slope steepness, and elevation. We calculated radiation at 1-minute intervals from sunrise to sunset and summed these values for 1 June to 31 August. We chose this 92-day period because we did not have an a priori prediction of the critical time for Grouseberry flower and fruit development and because the length of the growing season varies from year to year depending on weather and snow melt and among sites depending on microclimate.

We imposed an overshadowing function that set dPAR to zero when the height of obstacles on the solar azimuth blocked the sun by exceeding the solar altitude (Quaschning and Hanitsch 1998; Yard *et al.* 2005).

We used a clinometer (Suunto, Vantaa, Finland) and a Ranger sighting compass (Silva, Bromma, Sweden) to record the height (degrees of elevation above horizon) and horizontal sweep (compass bearings) of obstacles, whether geological features or fully closed canopy of coniferous foliage, for azimuths 50° through 310° (i.e., sunrise to sunset at the summer solstice). We recorded these data for each relatively homogeneous block of foliage or terrain; blocks ranged from 1° to several tens of degrees of horizontal sweep (block average 7.2°).

We imposed a second overshadowing function on the model to partly restrict dPAR because of the partial shade resulting from open coniferous canopy. We recorded the angular height and horizontal sweep, plus the average canopy openness in 5% increments from 5% for essentially closed canopy (sky almost completely obstructed; 5% of dPAR transmitted) to 95% for essentially no foliage (sky almost fully visible; 95% of dPAR transmitted), for each relatively homogeneous block of coniferous foliage (block average 18.2°), from azimuths 50° through 310°. Because these readings required subjective estimation of coniferous canopy density, all data were recorded by the same observer to avoid inter-observer variability.

These two procedures for estimating overshadowing often captured coniferous foliage up to 200 m away and, hence, were not equivalent to the "fish-eye" lens photographic method often employed in forest-gap studies (e.g., Englund *et al.* 2000).

We calculated dPAR at the 7-m and 13-m marks on our 20-m transects and averaged these to obtain one value per transect. Because comparisons among transects were relative in our analyses, we did not require absolute PAR values. Thus, we did not require continuous integration over the entire day, nor did we require locally corrected values for atmospheric parameters used by REST2 (we used REST2 default values).

We calculated only direct radiation (roughly 77–81% of total PAR, calculated for our transects using REST2 without overshadowing). Indirect PAR radiates from the entire sky, but not isotropically. Complex modeling of overshadowed, indirect, anisotropic PAR (Gueymard 1987) was beyond the scope of this study, as was measurement of the relatively minor shade created by shrubs and herbs.

Data analysis

Because of logistics associated with our remote sites, not all transects were established until 2009, and not all transects were monitored annually. In addition, we excluded 2007 data from our analyses, because that year many grouseberries on warm, south and west aspects ripened early and then became desiccated. When we began our counts, many fruits at warm sites had fallen, and other fruits fell to the ground when we touched the shrubs, becoming unrecognizable in the litter.

We scaled dPAR values relative to that from the transect with the largest dPAR value, which was set at 100. To avoid pseudoreplication, we combined the 22 transects at the prescribed burn sites into eight sampling units, i.e., the four burn sites and the four adjacent unburned forests, and we combined three transects at another site because they had essentially the same slope steepness, aspect, and forest cover. This produced 15 39 sampling units (transects or collapsed transects) for 2006–2012. Because the transects at the prescribed burn sites were reduced to four pairs of sampling units, we present differences in fruit densities between burned and unburned habitat using descriptive statistics.

Fruit densities were characterized by large variability, with numerous outliers. Therefore, we used robust regression analysis (R open-source software, version 3.0.2, WRS package) to assess the relation between fruit production and dPAR. This robust Theil-Sen based regression method uses bootstrap to analyze unconventionally distributed data and more accurately reflects trends in the data compared with ordinary least squares methods or nonparametric data transformations, which can give biased results (Wright and Field 2009).

Results

Annual fruit abundance

Based on 28 sampling units for which we had continuous records during 2008–2012, and scaling results relative to the year of highest fruit density (2010), we recorded relative Grouseberry fruit abundance of 22% in 2008, 35% in 2009, 100% (reference year) in 2010, 32% in 2011, and 48% in 2012. We also estimated relative abundance of 103% in 2006 based on 15 sampling units for which we had continuous records for 2006–2012.

Prescribed burns

In 2004, 3 years post-fire, Grouseberry fruit density in the burned transects averaged 0.17 times that in the adjacent, forested transects at the two sites we measured (Figure 2). The 2001 fires had burned the Grouseberry plants to ground level, and the plants were immature in 2004 (average Grouseberry height in the burns, 5.6 cm

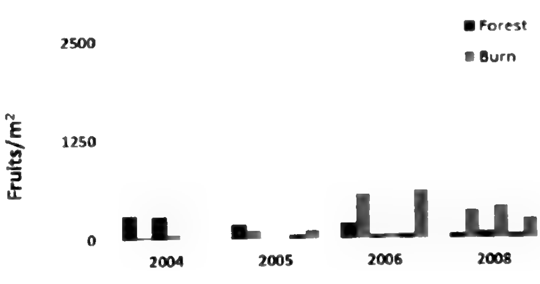

FIGURE 2. Grouseberry (*Vaccinium scoparium* Leiberg ex Coville) fruit production (fruits/m² of *Vaccinium* cover) during 2004–2008 at three prescribed burns conducted in Banff National Park, Alberta, during autumn 2001. Matched transects were located in adjacent, unburned forests. Data are missing for the third burn in 2004, the second burn in 2005, and all burns in 2007 when early fruit-fall invalidated counts.

[SD 0.9 cm] versus 12.7 cm [SD 1.9 cm] in the forests). In 2005, 4 years post-fire, results were mixed: one burn had 0.64 times the fruit density of the forested transects, whereas the second burn we measured had 2.3 times the fruit density of the forested transects.

In 2006 and 2008, 5 and 7 years post-fire, fruit densities in the three burns averaged 5.7 times and 4.8 times the densities recorded for the forested transects, respectively. There are no data for 2007, when early fruit-fall invalidated our counts.

In 2009, 8 years post-fire, fruit densities in the three west-facing burns averaged 0.41 times those in the forested transects, but at the east-facing site, fruit density in the burned transects was 10.1 times that in the adjacent, forested transects (Figure 3). During 2010–2012, fruit densities in the three west-facing burned transects were 3.3 times to more than 30 times those in the adjacent forested transects; those in the east-facing burned transects were 6.2 to more than 20 times those in the forested transects. Not all ratios are defined because the scarcity of fruits in some forested transects resulted in very small denominators and, thus, misleading ratios.

Relation between Grouseberry fruit density and site openness

Grouseberry fruit densities were positively associated with dPAR in 2006 and 2010–2012 ($P < 0.02$), but not in 2008 or 2009 ($P > 0.35$, Table 1). In 2010–2012, this positive relationship held whether the four sampling units in the prescribed burns were included or excluded ($P < 0.02$, Table 1). Figure 4 illustrates results for 2010, the year of highest fruit density.

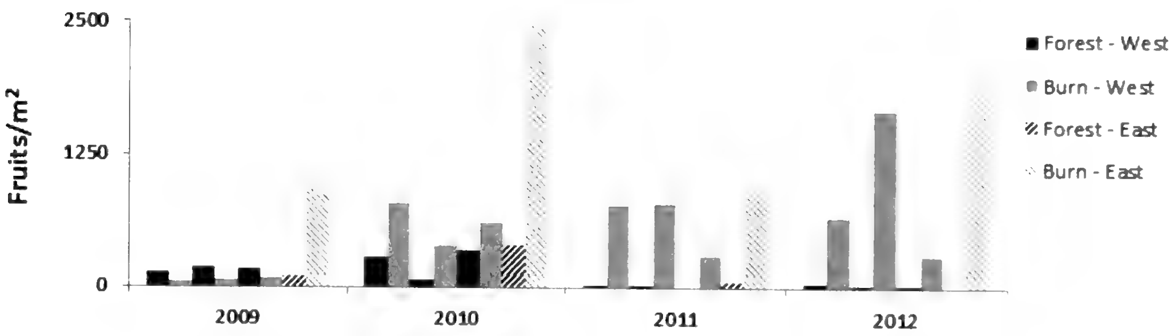

FIGURE 3. Grouseberry (*Vaccinium scoparium* Leiberg ex Coville) fruit production (fruits/m^2 of *Vaccinium* cover) during 2009–2012 at three west-facing prescribed burns and one east-facing prescribed burn conducted in Banff National Park, Alberta, during autumn 2001. Matched transects were located in adjacent, unburned forests.

TABLE 1. Association between Grouseberry (*Vaccinium scoparium* Leiberg ex Coville) fruit production and incoming direct photosynthetically active radiation including and excluding the four prescribed burn sites, Banff National Park, Alberta, 2006–2012.

Year	Intercept	Regression coefficient *b* (95% CI)	Explanatory power	*n*	*P*
Including prescribed burns					
2006	−412	11.25 (0.39 to 25.16)	0.45	15	0.017
2008	50	0.03 (−0.57 to 2.04)	0.00	34	0.354
2009	142	−0.65 (−2.37 to 2.42)	0.04	33	0.993
2010	−51	7.70 (4.65 to 14.04)	0.38	37	< 0.001
2011	−172	3.50 (0.33 to 8.29)	0.47	34	< 0.001
2012	−195	4.72 (2.16 to 9.01)	0.49	34	< 0.001
Excluding prescribed burns					
2006	579	14.93 (−7.72 to 15.72)	0.38	10	0.541
2008	61	−0.34 (−1.84 to 0.756)	0.05	27	0.514
2009	153	−0.90 (−4.18 to 1.83)	0.04	28	0.541
2010	30	5.84 (2.51 to 12.99)	0.21	31	< 0.001
2011	−52	1.24 (0.15 to 5.69)	0.21	28	0.015
2012	−114	3.16 (1.09 to 6.54)	0.34	28	0.007

Note: CI = confidence interval.

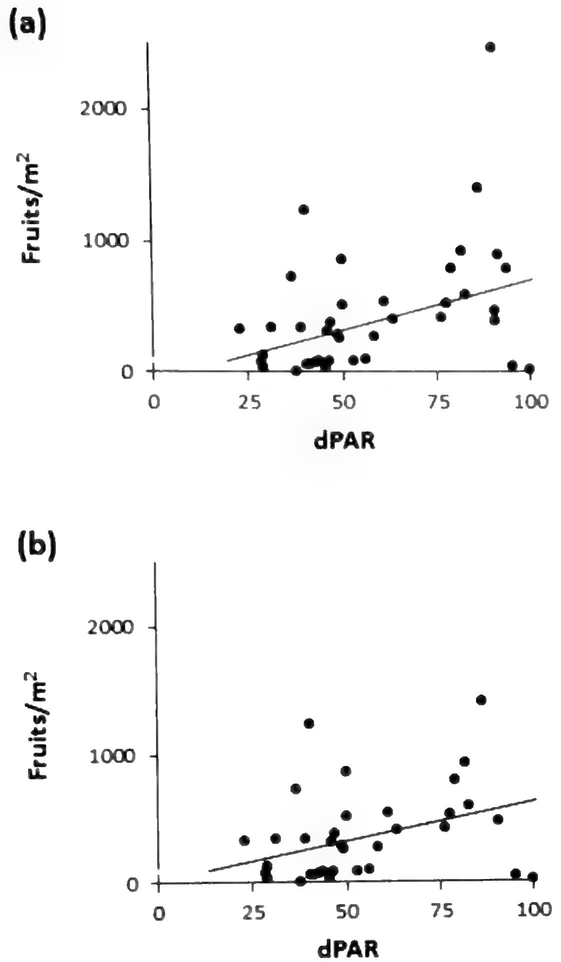

FIGURE 4. Relation between Grouseberry (*Vaccinium scoparium* Leiberg ex Coville) fruit production (fruits/m^2 of *Vaccinium* cover) in 2010 and direct photosynthetically active radiation adjusted for overshadowing by topography and conifer foliage and summed for the 92-day period from 1 June through 31 August in Banff National Park, Alberta, including the four prescribed burns (a) and excluding the four prescribed burns (b). The best-fit lines were derived from Theil-Sen robust regression.

Discussion

We recorded high Grouseberry fruit densities in the open sites created when the 2001 prescribed fires removed the forest canopy. During 2006–2012, fruit densities at the burn sites were 3.3 to more than 30 times those in the adjacent forest except in 2009 when density was high only in the east-facing burn site (Figures 2, 3). Similarly, Weaver *et al.* (1990) reported that Grouseberry fruit production at a site where the Whitebark Pine (*Pinus albicaulis* Engelmann) canopy had been removed was 6 times that in two adjacent forests. High fruit production at sites where fire, logging, avalanching, or other factors have removed the forest overstory is common for many fruiting species (Lindzey *et al.* 1986; Hamer 1996; Greenberg *et al.* 2007; McCord *et al.* 2014).

We attribute the fact that, 3 and 4 years following fire, fruit production was lower in the west-facing prescribed burns than the adjacent forests in three of the four cases (Figure 2) to the time required for Grouseberry shrubs to re-establish following fire. The fires removed the above-ground portions of the Grouseberry shrubs and left a black scorched surface layer. Five years post-fire, however, the burned transects produced 5.7 times more fruits than the transects in the adjacent forests. A Buffaloberry (*Shepherdia canadensis* [L] Nuttall) study in the same valley of Banff National Park also found a 5-year lag in fruit production following prescribed fire (Hamer 1996).

Changes in soil nutrient status can occur following fire. However, in our prescribed burns, by 2012 (11 years post-fire), the fires' effects on nutrient cycling may have been minimal. The effect on nutrients can be greatest immediately following fire, but nitrogen can return to pre-fire levels in a few years and phosphorus in a few months; effects on other nutrients can be even more ephemeral (Certini 2005). We did not conduct soil or nutrient analyses for our study area.

We found a positive relation between Grouseberry fruit density and dPAR in 4 of the 6 years analyzed (Table 1). There was no significant relation in the 2 years of lowest fruit production. For 2010–2012, these positive relations held, with or without the prescribed burn sites included in the analysis, and, hence, were not simply driven by the higher fruit production we found in the prescribed burns following the 5-year lag in post-fire recovery. In 2006, the relation between dPAR and fruit density did not hold when the burns were excluded, but this analysis is based on only 10 sampling units because several study sites had not yet been established.

When measuring fruit density, we subjectively repositioned our quadrats (normally by a few decimetres or less) from the 2-m marks along transects when necessary to ensure high cover of *Vaccinium* inside the frame. We also converted these counts to a 100% *Vaccinium* cover basis to standardize fruit densities among sites and observers. Thus we measured relative or ecological fruit density per square metre of *Vaccinium* cover, not absolute fruit density per hectare of habitat. This approach emulates the behaviour of frugivores, which can forage with high efficiency by moving from shrub to shrub (patch to patch).

Although we recorded high fruit densities at the four burn sites we studied, we searched seven other prescribed burns in Banff National Park, but did not find sufficient *Vaccinium* cover for sampling. These other burns were typically in warmer habitat at lower elevations where there was a high cover of grasses and other herbs. We also recorded low Grouseberry fruit densities in some open but xeric, south-facing habitat. This included an open, xeric, south southwest-facing transect with the highest dPAR value of our study. During 2008–2012, this transect averaged 0.29 times the fruit density of a second transect located 20 m away

under more mesic conditions associated with 40% forest canopy cover. Keefer *et al.* (2010*) reviewed studies on Huckleberry that similarly found reduced fruit production in fully open sites. We also recorded fruit densities that were 5 or more times and 3 or more times higher in the more mesic east-facing prescribed burn site than in west-facing burn sites in 2009 and 2010, and equal or greater densities in 2011 and 2012 (Figure 3). Although this observation is based on only one east-facing burn site, it is consistent with observations from Huckleberry studies. For example, Martin (1983) found that the most productive Huckleberry sites were in north- and east-facing burn sites. Similarly, the highest fruit densities recorded in a Buffaloberry study in Banff National Park were on north northeast-aspect slopes (Hamer 1996). A positive influence of mesic site conditions on fruit production was also suggested by Burton (1998*), who reported a stronger relation between Huckleberry fruit production and site moisture conditions, than between fruit production and solar radiation.

Our study did not specifically address the effects of mesic site conditions given that it was limited in extent (to 39 or fewer sampling units), focused on dPAR, and did not permit a more comprehensive multivariate analysis. Nevertheless, we have shown that Grouseberry fruit production increases with increasing site openness and that moderate to high fruit production can be restored when prescribed fire is applied in appropriate habitat types.

Many of the prescribed fires in Banff National Park have been on warmer slopes (e.g., south and west aspect) and more often in the lower subalpine than in the upper subalpine or near the treeline. When prescribed fire is used on these warmer, drier slopes, the post-fire community is often dominated by grasses. In contrast, historic wildfires that burned through mesic, upper subalpine habitat near the treeline have, in some cases, led to extensive, open Grouseberry communities. Our study documents the ecological benefits of both high-elevation prescribed burns and wildfire in forests where Grouseberry shrubs are widespread but fruit production is low under the forest canopy.

Acknowledgements

This project was supported by Parks Canada, the Banff National Park Resource Conservation Service, and Northern Lights College. Chris Gueymard made his solar radiation computer programs available to us and provided suggestions; and Mark Roberts developed our computer program with overshadowing functions. We also thank B. Chruszcz, A. Forshner, H. Galt, S. Herrero, A. Kortello, B. Low, S. Michel, R. Osiowy, J. Park, L. Pengelly, S. Rasheed, A. Schultz, L. Wiggins, M. Woode, N. Woode, D. Zell, and anonymous reviewers for assistance.

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Received 1 April 2014
Accepted 2 July 2014

Song Discrimination by Male Mourning Warblers (*Geothlypis philadelphia*) and Implications for Population Divergence across the Breeding Range

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Pitocchelli, Jay. 2014. Song discrimination by male Mourning Warblers (*Geothlypis philadelphia*) and implications for population divergence across the breeding range. Canadian Field-Naturalist 128(4): 408–415.

Geographic variation in song may reduce or eliminate the ability of some populations to recognize each other as conspecifics, possibly leading to assortative mating, reproductive isolation, and speciation. Song playback experiments, used to evaluate the significance of geographic variation in song, have been particularly useful in discovering divergence among previously unknown populations of sibling species. In this study, I report the results of song playback to male Mourning Warblers (*Geothlypis philadelphia*) from populations throughout the breeding range and discuss the implications for population divergence. Four regions in the breeding range contain unique song types or regiolects: western, eastern, Nova Scotia, and Newfoundland. Results of reciprocal song playback experiments showed that males from the western and Newfoundland regiolects respond more aggressively to songs in their own regiolect than those in the other regiolects. Interior populations, i.e., eastern and Nova Scotia regions, showed little or no difference in aggressive response toward their own versus other regiolects. This pattern may be due to a combination of geographic proximity of populations belonging to different regiolects, song learning, experience, and contact during migration. Song discrimination by populations from the western Prairie Provinces and Newfoundland is consistent with the existence of at least partial reproductive isolation at the geographic extremes of the breeding range.

Key Words: Mourning Warbler; *Geothlypis philadelphia*; song; playback experiment; song discrimination

Introduction

Birdsong is a reproductive display recognized by a network of males and females of the same species (Paterson 1985; McGregor and Dabelsteen 1996). It is regarded as one of the most compelling examples of a prezygotic isolating mechanism (Remsen 2005; Hall and Hallgrimsson 2008). Because birdsong plays such an important role in maintaining reproductive cohesion among populations of the same species, instances of gradual divergence, such as geographic variation, may challenge the ability of birds to recognize songs from different parts of the breeding range leading to reproductive isolation and speciation (Edwards *et al.* 2005; Price 2008). Geographic variation in oscine songbirds is well known and has been described at two spatial scales (see reviews of Mundinger 1982; Podos and Warren 2007). Song differences between contiguous populations separated by short distances and capable of interbreeding is referred to as microgeographic or dialect variation. Macrogeographic or regiolect variation occurs where large regions of the breeding range contain unique song types.

In an article on the role that song variation plays in species-level classification, Remsen (2005) asked how much variation in song is required to exceed the limits of species recognition, create barriers to gene flow, and result in speciation. Studies of geographic variation in song coupled with playback experiments present an opportunity to address this issue. Playback experiments with territorial males have been used to test hypotheses about song discrimination in many species at the dialect and regiolect levels (Baker *et al.* 1981; Searcy *et al.* 1997; Price 2008). Similarly, song playback experiments have been performed on captive females, implanted with estradiol, to test female discrimination of song types from different parts of the breeding range (Balaban 1988; Searcy 1992; Searcy *et al.* 2002; Anderson 2009; Danner *et al.* 2011).

A general result of playback studies at the dialect and regiolect levels is evidence that members of both sexes are capable of song discrimination. Males react more aggressively to homotypic or local songs shared with their neighbours compared with foreign or heterotypic songs from different parts of the breeding range. Females respond more favourably to homotypic songs (Price 2008). Research on the effects of song variation and discrimination on gene flow has been mixed. Studies at the microgeographic level have shown that dialects do not act as barriers to gene flow in the Yellow-naped Parrot (*Amazona auropalliata*; Wright and Wilkinson 2001), the White-crowned Sparrow (*Zonotrichia leucophrys*; Soha *et al.* 2004), and the Brown-headed Cowbird (*Molothrus ater*; Fleischer and Rothstein 1988). However, genetic and morphologic divergence have been correlated with song differences among subspecies of the Swamp Sparrow (*Melospiza georgiana*; Liu *et al.* 2008) and regiolects in several Palearctic species belonging to the genera *Parus* and *Phylloscopus* (Helbig *et al.* 1996; Martens 1996; Irwin *et al.* 2001).

In this paper, I report the results of song playback experiments with territorial male Mourning Warblers (*Geothlypis philadelphia*). This species is monotypic, with a large breeding range extending over much of

Canada and parts of the eastern United States (Mayr and Short 1970; Pitocchelli 2011a). There is a well-defined pattern of geographic variation in songs, with four regiolects: western, eastern, Nova Scotia, and Newfoundland. Songs of males within each regiolect are very similar; variation within a regiolect is usually minor and involves the omission or substitution of a single syllable. A zone of admixture exists in western Ontario, Minnesota, and Wisconsin where males from both the western and eastern regiolects breed. Hybrid songs containing a mix of western and eastern syllable types have been recorded in this zone (Pitocchelli 2011b). Although geographic variation in song exists, it is unknown to what degree these song differences are recognized by populations of each regiolect.

I conducted a series of reciprocal playback experiments within the geographic boundaries of each regiolect to test three hypotheses. First, populations within each regiolect discriminate between songs from all of the other regiolects. The prediction from this hypothesis is that the responses of males will be more aggressive toward playback of homotypic songs from the same regiolect versus heterotypic songs of each of the other regiolects. Second, populations within each regiolect are partly capable of song discrimination. The prediction here is that there will be higher levels of aggression by males to homotypic songs versus heterotypic songs of some but not all of the other regiolects. Third, populations within each regiolect do not discriminate between homotypic songs and heterotypic songs of any of the regiolects. The prediction from this hypothesis is that males within each regiolect show equal levels of aggression toward homotypic and heterotypic songs. The results of this study show that response differences and song discrimination do occur, but are not consistent throughout the breeding range. I discuss the effect of geographic proximity on the pattern of song discrimination and the implications of song discrimination for reproductive isolation among breeding populations.

Study Area

I selected study sites for playback experiments within the geographic boundaries defining each regiolect: western, eastern, Nova Scotia, and Newfoundland (Figure 1). Latitude and longitude of study sites were Hudson Bay, Saskatchewan, 53.96°N, 102.35°W; Duck Mountain Provincial Park, Manitoba, 51.89°N, 100.85°W; Marathon, Ontario, 48.68°N, 86.10°W; Twin Mountain, New Hampshire, 44.20°N, 71.70°W; Oxbow, Maine, 46.33°N, 68.42°W; Wreck Cove, Nova Scotia, 46.08°N, 60.80°W; and Stephenville Crossing, Newfoundland, 48.60°N, 58.35°W.

Methods

Approximately 30 focal males from each regiolect were evenly divided into three experimental groups (Table 1). Group I was presented with homotypic songs from their own regiolect and heterotypic songs from one of the foreign regiolects (e.g., western focal males presented with western versus eastern songs). Group II

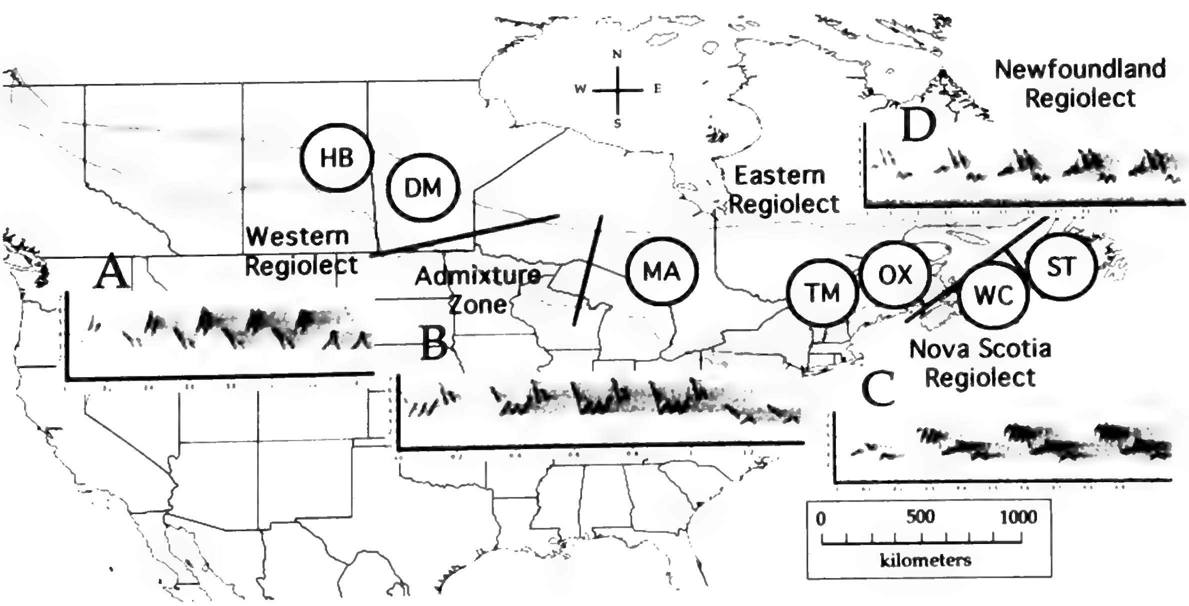

FIGURE 1. Distribution of the four regiolects of the Mourning Warbler (*Geothlypis philadelphia*), locations of the playback experiments, and sample songs from: A, the western regiolect; B, the eastern regiolect; C, the Nova Scotia regiolect; and D, the Newfoundland regiolect. Western study sites were Hudson Bay, Saskatchewan (HB) and Duck Mountain Provincial Park, Manitoba (DM); eastern study sites were Marathon, Ontario (MA), Twin Mountain, New Hampshire (TM), and Oxbow, Maine (OX); the Nova Scotia study site was Wreck Cove (WC), and the Newfoundland study site was Stephenville Crossing (ST). Shaded region indicates distribution of breeding range.

TABLE 1. Design and number of playback experiments to test song discrimination by Mourning Warblers (*Geothlypis philadelphia*) throughout their breeding range.

Playback locality	Focal male's song*	Regiolect of playback songs (n)	Mean difference in Principal Component 1 Scores (95% CI)	Level of significance Student's t test†
Western regiolect (WR): Hudson Bay, Saskatchewan; Duck Mountain Provincial Park, Manitoba	WR	Group I: WR vs. ER (9)	0.46 (0.39)	$P = 0.026$‡
		Group II: WR vs. NSR (10)	1.72 (0.67)	$P < 0.001$
		Group III: WR vs. NFR (10)	0.99 (0.58)	$P = 0.004$
Eastern regiolect (ER): Marathon, Ontario; Twin Mountain, New Hampshire; Oxbow, Maine	ER	Group I: ER vs. WR (11)	0.38 (0.67)	$P = 0.238$§
		Group II: ER vs. NSR (10)	1.16 (0.68)	$P = 0.004$
		Group III: ER vs. NFR (9)	0.99 (1.16)	$P = 0.085$§
Nova Scotia regiolect (NSR): Wreck Cove	NSR	Group I: NSR vs. WR (10)	0.00 (1.18)	$P = 0.997$§
		Group II: NSR vs. ER (12)	0.48 (0.58)	$P = 0.095$§
		Group III: NSR vs. NFR (10)	−0.04 (0.79)	$P = 0.913$§
Newfoundland regiolect (NFR): Stephenville Crossing	NFR	Group I: NFR vs. WR (10)	1.67 (0.64)	$P < 0.001$
		Group II: NFR vs. ER (10)	1.08 (0.62)	$P = 0.003$
		Group III: NFR vs. NSR (10)	1.27 (1.06)	$P = 0.024$‡

Note: CI = confidence interval.
*Confirmed by digital recordings.
†Two-tailed comparison; null hypothesis is that the mean difference is equal to zero.
‡ Not significant after sequential Bonferroni correction.
§Not significant.

was challenged with homotypic songs and heterotypic songs from a different regiolect (e.g., western focal males presented with western versus Nova Scotia songs). Group III was challenged with homotypic songs and heterotypic songs from the remaining regiolect (e.g., western focal males presented with western versus Newfoundland songs). To ensure that multiple stimuli represented a class of stimuli and to minimize pseudoreplication (Kroodsma 1989; Kroodsma *et al.* 2001), each focal male was presented with a unique combination of different, randomly selected homotypic and heterotypic songs. I selected 30 western, 30 eastern, 30 Nova Scotia, and 30 Newfoundland exemplar songs for this study. Each song was from a different male. I made the selections based on the best recordings from earlier work on this species (Pitocchelli 1988, 1990, 2011b).

I used the simultaneous, two-speaker presentation of auditory stimuli model for playback experiments (Lanyon 1978). Simultaneous presentation of different song types tests the comparative prioritization of responses and reveals which song is perceived to be a greater threat to a territorial male (Darren Irwin, Biodiversity Research Centre and Department of Zoology, University of British Columbia, 7 April 2014, personal communication). I placed two PureFi Anywhere speakers (Logitech, Lausanne, Switzerland) approximately 30 m apart (positions 1 and 2), on either side of the first song post that I observed for each male. I assumed that this song post was within the territory of the focal male. The speakers were each connected to an iPod (Apple Inc., Cupertino, California, USA). For the first four minutes of the experiment (Period I), regiolect A was played at position 1 while regiolect B was played at position 2 (A and B representing any randomly selected pair of homotypic and heterotypic songs; Figure 2). After two minutes of silence, I conducted another four minute presentation (Period II) with the same songs but with positions reversed, i.e., regiolect B was played at position 1 while regiolect A was played at position 2). Approximately 19 homotypic and 19 heterotypic songs were presented during each four-minute period, which simulated the average natural rate of one song per 13 seconds by territorial males.

The songs were digitized and assembled using Raven Pro version 1.4 for Mac OSX (Cornell Lab of Ornithology, Bioacoustics Research Program, Ithaca, New York, USA) and iTunes version 8.2.1 (Apple Inc.). Homotypic and heterotypic songs were arranged so that they did not overlap and males could clearly hear all songs during the experiment. When necessary, I manipulated the songs using the amplify settings in Raven so that they were all similar in amplitude. All experiments were performed from 6 to 11 a.m. in June 2008, 2009, and 2010.

I used four response variables to measure aggressive behaviour of the focal males toward either homotypic or heterotypic songs: 1) number of flights toward and/or over a speaker, 2) number of chip notes directed toward a speaker, 3) number of songs directed toward a speak-

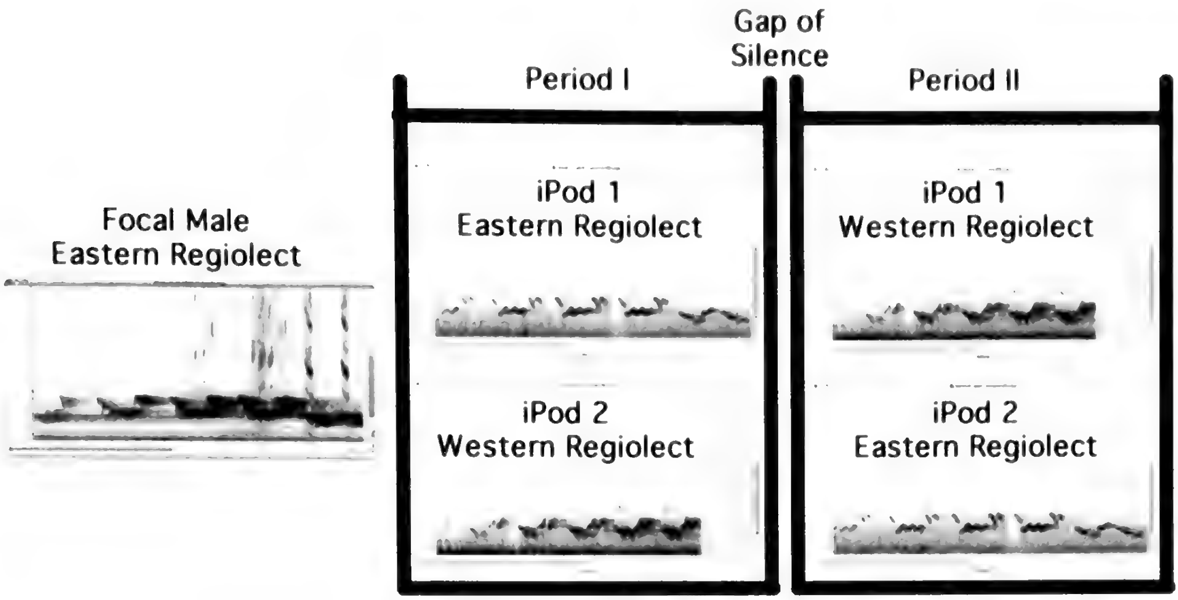

FIGURE 2. Experimental setup for an eastern focal male Mourning Warbler (*Geothlypis philadelphia*) and his song type challenged by playback of homotypic eastern regiolect and heterotypic western regiolect songs. Periods I and II were four minutes long and separated by two minutes of silence.

er, and 4) time spent within 3 m of a speaker. For each focal male, the responses to the homotypic song for Period I and Period II were combined, as were the responses to the heterotypic song for Periods I and II.

Before statistical analysis, I transformed the response data following guidelines in Zar (2010) to avoid deviations from normality and to account for the large number of zero data entries often encountered in playback experiments (Balakrishnan and Sorenson 2006). Number of flights, number of chip notes, and number of songs were square root transformed. The time spent within 3 m of a speaker was $\log_{10}$ transformed, $\log_{10}(x + 1)$. I subjected the transformed data to a principal components analysis to reduce the correlated variables to a new set of uncorrelated principal component (PC) scores (Martin and Martin 2001; Balakrishnan and Sorenson 2006). Each male received a PC score based on its combined responses to a homotypic song during Periods I and II. A separate PC score was calculated from the combined responses to the heterotypic song during Periods I and II. I chose scores for the first PC (PC1) for subsequent statistical tests because PC1 explained 71.4% of the variation and it was also the best index of aggression. All response variables were positive for PC1: number of flights (0.67), number of chips (0.98), number of songs (0.02), and time spent within 3 m of the speaker (0.24). Higher PC1 scores indicated higher levels of aggression toward a song type.

I chose a paired samples Student's t test to analyze these data because each focal male was exposed to two treatments: playback of homotypic songs and playback of heterotypic songs. This test determines whether the average difference between PC1 scores for homotypic and heterotypic songs is significantly different from zero for each group in a regiolect. Differences significantly greater than zero indicated a stronger response to the homotypic song, whereas differences significantly less than zero indicated higher levels of aggression toward heterotypic songs. Significant differences in either direction were considered to be evidence of song discrimination. The absence of a significant difference from zero indicated equal levels of aggression toward homotypic and heterotypic songs and was interpreted as an inability to discriminate between these songs.

I performed three paired samples Student's t tests, one for each group (I, II, III) in each regiolect (Table 1). The design produced a total of 12 statistical tests. The differences for PC1 scores did not deviate from a normal distribution for 10 of the 12 statistical tests, which meets a critical assumption of the paired samples Student's t test (Zar 2010). In cases where multiple statistical tests are used, Rice (1989) recommended using a sequential Bonferroni adjustment to correct for possible inflation of probability levels. I began the sequential Bonferroni application with an alpha level indicating a significant difference at $P \leq 0.0042$ (P = 0.05/12 Student's t tests). The use of this adjustment has been controversial (Moran 2003), so I have presented the results with and without the correction in Table 1. I also discuss these specific instances in the Results and Discussion sections below.

Results

The results of the paired samples Student's t tests were mixed. Aggressive responses toward homotypic songs and heterotypic songs were significantly differ-

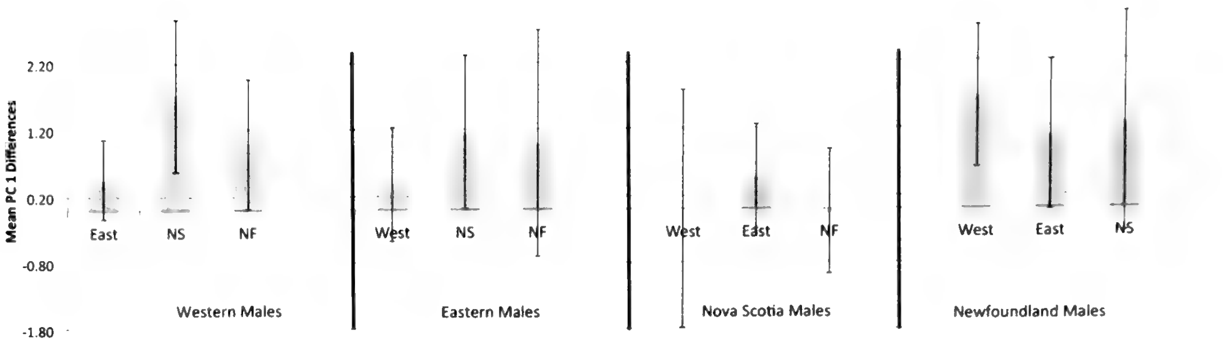

FIGURE 3. Mean differences in first principal component (PC1) scores between responses to homotypic and heterotypic songs by focal male Mourning Warblers (*Geothlypis philadelphia*) within each regiolect. Error bars are confidence intervals that reflect sequential Bonferroni-corrected alpha values. West = western regiolect, East = eastern regiolect, NS = Nova Scotia regiolect, NF = Newfoundland regiolect.

ent among males from extreme western and eastern parts of the breeding range. But interior populations from the eastern and Nova Scotia regiolects showed little or no differences in level of aggression toward homotypic and heterotypic songs (Table 1, Figure 3).

For males singing the western regiolect in the Prairie Provinces, results from Student's t tests suggest complete song discrimination. Western males responded more strongly to homotypic songs compared with heterotypic songs from Nova Scotia ($t = 5.79$, two-tailed, df = 9, $P < 0.001$) and Newfoundland ($t = 3.87$, two-tailed, df = 9, $P = 0.004$) regiolects. The results suggest that western males also responded more aggressively to homotypic songs versus the eastern regiolect, but the comparison was not significant after employing the sequential Bonferroni correction ($t = 2.74$, two-tailed, df = 8, $P = 0.026$).

The Student's paired t test results for eastern males (Table 1, Figure 3) supported the partial song discrimination hypothesis. Eastern males responded more aggressively to homotypic songs versus heterotypic songs from Nova Scotia ($t = 3.85$, two-tailed, df = 9, $P = 0.004$). But there were no significant differences in responses to homotypic and heterotypic songs from the western ($t = 1.26$, two-tailed, df = 10, $P = 0.238$) or Newfoundland ($t = 1.99$, two-tailed, df = 8, $P = 0.085$) regiolects.

The results from experiments with Nova Scotia males supported the third hypothesis of no song discrimination (Table 1, Figure 3). There were no significant differences in response to their own songs versus songs from the western ($t = 0.004$, two-tailed, df = 9, $P = 0.997$), eastern ($t = 1.83$, two-tailed, df = 11, $P = 0.095$), and Newfoundland ($t = -0.11$, two-tailed, df = 9, $P = 0.913$) regiolects.

In contrast, the results for Newfoundland males suggested complete discrimination (Table 1, Figure 3), similar to that found in western males. The differences in responses by Newfoundland males toward homotypic songs compared with heterotypic songs from the western ($t = 5.85$, two-tailed, df = 9, $P < 0.001$) and eastern ($t = 3.93$, two-tailed, df = 9, $P = 0.003$) regiolects were significant. In both cases, males responded more aggressively toward homotypic songs. Although there also was a difference between responses to homotypic versus Nova Scotia regiolects by these males ($t = 2.70$, two-tailed, df = 9, $P = 0.024$), it was not significant after the sequential Bonferroni correction.

Discussion

These results for song discrimination by the Mourning Warbler are in general agreement with previous studies of song playback experiments in other species where males exhibited higher levels of aggression toward local, homotypic songs than heterotypic songs from distant parts of the breeding range (Regelski and Moldenhauer 1996; Searcy *et al.* 1997; Dufty and Hanson 1999; Nelson and Soha 2004; Price 2008). However, not all populations discriminated between homotypic and heterotypic songs (Table 2). Mourning

TABLE 2. Ability of focal males to discriminate among songs of other Mourning Warblers (*Geothlypis philadelphia*) from four regiolects within the species' breeding range. No discrimination = no significant difference in responses to homotypic and heterotypic songs; Discrimination = significant difference in responses to homotypic and heterotypic songs; Equivocal = $P < 0.05$ based on Student's t tests, but not significant after sequential Bonferroni correction.

Regiolect of focal male	Response to regiolect of playback song			
	Western	Eastern	Nova Scotia	Newfoundland
Western	—	Equivocal	Discrimination	Discrimination
Eastern	No discrimination	—	Discrimination	No discrimination
Nova Scotia	No discrimination	No discrimination	—	No discrimination
Newfoundland	Discrimination	Discrimination	Equivocal	—

Warbler males at the extremes of the breeding range showed the highest levels of discrimination by responding more aggressively to homotypic than heterotypic songs. Males from the western and Newfoundland regiolects could discriminate between their own songs and at least two of the other regiolects. They may also recognize differences for the remaining regiolects but the Student's *t* test results were not significant after the sequential Bonferroni correction. These findings support the hypothesis of complete discrimination by populations at the extreme eastern and western parts of the breeding range.

Song discrimination by interior populations of the eastern regiolect was weaker and supported the partial discrimination hypothesis. Eastern males discriminated between eastern songs and the Nova Scotia regiolect. However, they did not discriminate behaviourally between homotypic songs and the neighbouring Western regiolect or between homotypic songs and the Newfoundland regiolect. The results for the Nova Scotia experiments supported the complete lack of discrimination hypothesis. These males showed equal levels of aggression toward homotypic and heterotypic songs when challenged with songs from all of the other regiolects.

One explanation for the spatial pattern of discrimination by Mourning Warbler males is a combination of the effects of geographic proximity and song learning. Repeated exposure and song learning have been shown to modify song recognition among and within species (Irwin and Price 1999; MacDougall-Shackleton *et al.* 2001; Price 2008). If geographic proximity and experience influence song discrimination in Mourning Warblers, then we should observe two different results from these playback experiments. Allopatric populations separated by large distances should exhibit song discrimination because there is no contact or opportunity to learn each other's songs. In contrast, sympatric populations should show little or no discrimination because of geographic proximity and previous experience with different song types that they may later recognize as equally potent threats to territorial ownership.

Males from the western and Newfoundland populations were mutually capable of song discrimination between their regiolects. Results for these allopatric populations support the idea that a lack of contact and experience with songs leads to song discrimination. The inconsistent patterns of discrimination by populations from the interior of the breeding range appear to support the contention that populations in close proximity may not discriminate among different songs. For instance, eastern males did not recognize differences in western songs and these populations overlap in a large admixture zone in the western Great Lakes region. However, the role of geographic proximity is still unclear for these interior populations.

The playback experiments within the western and eastern regiolects were outside the admixture zone (Figure 1), so it is unclear why males from New Hampshire and Maine could recognize the western regiolect as a threat equal to eastern songs from other locations. Another problem arises from results where allopatric populations were not able to discriminate between homotypic and heterotypic songs. Eastern and Newfoundland populations are separated by the Gulf of St. Lawrence but eastern males responded equally to both song types. Nova Scotia and western populations are also allopatric, but Nova Scotia males reacted strongly to western songs. An alternative explanation for some of these inconsistencies in song discrimination is that the divergence among song types from the eastern and Nova Scotia regiolects is too recent and does not exceed the limits of recognition by these males. Although Pitocchelli (2011b) found statistical differences in syllables and physical parameters of these songs, males still recognize them as a threat to territorial ownership.

Playback experiments that show song discrimination among different populations have been cited as evidence of reproductive isolation (Balakrishnan and Sorenson 2006; Danner *et al.* 2011). Irwin and colleague's (2001) study of mitochondrial DNA differences among populations of Old World Leaf Warblers (*Phylloscopus* spp.) confirmed reproductive isolation that paralleled evidence from playback experiments. Studies of mitochondrial DNA and playback experiments on Chiffchaff superspecies (*Phylloscopus*) produced similar results (Helbig *et al.* 1996; Martens 1996). If song discrimination by Mourning Warblers also indicates prezygotic isolation, then populations from the Prairie Provinces may be reproductively isolated from allopatric populations in Nova Scotia and Newfoundland. Newfoundland populations may also be reproductively isolated from continental populations based on successful discrimination of their songs from songs of the western and eastern regiolects.

Although these results suggest prezygotic isolation between some populations, additional playback experiments with females (if possible) would be informative. Relying on male responses alone may not always indicate isolation between different song populations. Danner *et al.* (2011) found gender differences in Rufous-collared Sparrow's (*Zonotrichia capensis*) responses to homotypic and heterotypic songs. Males did not differ in their responses to homotypic or heterotypic dialects, while females reacted more strongly to the local, homotypic songs. The pattern of female responses to different dialects was correlated with genetic differences between populations while male responses were not. Relying on evidence from male responses alone would not have revealed this divergence. Analyses of mitochondrial DNA and nuclear DNA from Mourning Warblers in each regiolect would ultimately be necessary to clarify actual levels of pop-

ulation divergence and whether genetic divergence is correlated with song differences in this species.

Acknowledgements

This work was funded in large part by a summer research grant from Saint Anselm College. I thank the staff at the Geisel Library, especially Jeff Waller, Sue Gagnon, and Sam Urtz, for their help with procuring books and journal titles through inter-library loan. The manuscript benefited from insightful comments provided by Darren Irwin, Robert Rockwell, and two anonymous reviewers. I also thank Joe Troisi, Kathy Flannery, and Lori LaPlante for discussions and suggestions regarding experimental design and appropriate statistical analyses.

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Received 8 May 2014
Accepted 20 July 2014

Book Reviews

Book Review Editor's Note: We are continuing to use the current currency codes. Thus Canadian dollars are CAD, U.S. dollars are USD, Euros are EUR, China Yuan Remimbi are CNY, Australian dollars are AUD and so on.

Zoology

Amphibian Conservation – Global Evidence for the Effects of Interventions

By Rebecca K. Smith, and William J. Sutherland. 2014. Pelagic Publishing, PO Box 725, Exeter, UK, EX1 9QU. 279 pages, 29.99 GBP, Paper.

This comprehensive British synopsis was prepared with funding by Synchronicity Earth and Aria. It is the fourth volume in the Synopses of Conservation Evidence series and is linked to the online www.conser vation evidence.com where the full text is available without charge as an alternative to paying for it in print. Its dense text summarizes and discusses selected world studies concerned with the results, positive and negative, of tampering with natural populations. These have been usually well-meaning attempts to compensate for the damage done by expanding human populations. Impacts may have been either direct by past eradication of individuals or indirect through destruction or alteration of habitats critical to the survival of one or more amphibian species.

The introduction stresses that this survey is intended to influence those in a position to make decisions that could save biodiversity one case at a time. Although recommendations are not provided, basic ecology is included. Interventions that are discussed are not ranked by importance or extent of their effects or evaluated by their quality. The multitudes of references to publications of many countries are grouped with the headings where they are appropriate.

The text is broken into 14 sections each with *key messages* and various subheadings. Ten concentrate on threats: residential and commercial development (*interventions specific to development)*; agriculture (*engage farmers and other volunteers, terrestrial and aquatic habitat management);* energy production and mining (*mist habitat*); transportation and service corridors (*install culverts or tunnels, barrier fencing, modify drains and kerbs, signs and road closures, assistance during migration*); human intrusions and disturbance (*signs and access restriction*); natural system modifications (*prescribed fire, herbicides, mechanical removal of vegetation, regulate water levels*); invasive alien and other problematic species (*reduce predation, competition and habitat alteration by other species, reduce parasitism and disease by chytridiomycosis and ranaviruses*); pollution (*agricultural and industrial*); climate change and severe weather (*irrigation, ephemeral ponds, shelter habitat, gradients*). These are followed by habitat protection (*connectivity, buffer zones*); habitat restoration and creation (*terrestrial, aquatic*); species management (*translocate, captive breeding, rearing, release*); education and awareness raising (*campaigns, programs, citizen science*).

A 17-page index concludes the book but is a disappointment. Canadian studies are not cited by country or province forcing the reader to search through the text for references to them. However, there are entries for other countries and many entries by species.

This is part of an ambitious series that aims toward accumulating a comprehensive summary of evidence on the effects of conservation interventions on saving the diversity of life over the entire planet. Among other titles completed is *Bee, Bird, Farmland* and more are being prepared to cover different groups and habitats.

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Amphibians and Reptiles in Minnesota

By John J. Moriarty, and Carol D. Hall. 2014. University of Minnesota Press, Suite 290 111 Third Avenue South, Minneapolis, MN, USA, 55401. 372 pages, 39.95 CAD, Paper.

This new survey of the Minnesota herpetofauna comprehensively updates *Amphibians and Reptiles Native to Minnesota* by Barney Oldfield and John J. Moriarty (1994; reviewed by FRC 1998 Canadian Field-Naturalist 112(1): 170–171). The extent of new information now available is reflected in a Resources section which includes 6 Minnesota, 6 Regional (Upper Midwest), 12 North American, and 8 General references published since the earlier treatment. This is further emphasized in the Literature Cited, which has 144

post-1994 entries in its 20-page coverage (included are some duplications from the more general Resources listings).

Minnesota lies to the south of the boundaries of western Ontario and Manitoba. It has a primarily northeastern and east-central North American herpetofauna so it is not surprising that of the 53 species recorded for the state, 48 are shared with Canada. The representation of the two classes is unbalanced as there are more shared reptiles but many barely enter Canada whereas, in contrast, many of the fewer shared amphibian species present have moved extensively into the north. In all, 22 amphibians (14 frogs and toads and 8 salamanders), and 26 reptiles (2 lizards, 16 snakes and 8 turtles) recorded also occur in Canada. For seventeen (1 frog, 1 toad, 3 salamanders, 1 lizard, 8 snakes, 3 turtles) that are shared with Canada the Minnesota occurrences are not linked to Manitoba or northeastern Ontario but to populations south of the Great Lakes. Three of the species now included have been added to the state list from the eastern part of Minnesota since 1994 and it is suggested that three additional species (1 frog, 1 toad and 1 spadefoot) that occur near the western border of the state may yet be found within it. One of these occurs in Manitoba.

The contents open with a map of Minnesota counties with arbitrary divisions of the large northeast counties (this map is copied for quick referenced on the inside back cover). A forward stresses the varied interests which this book serves. A preface and acknowledgments deal with the herpetological activity in the state and the growth of interest in conservation. An introduction covers the definition of "herp", the history of herpetology in Minnesota, the Minnesota Department of Natural Resources Nongame Wildlife Program, Minnesota Herpetological Society, and other herpetological efforts, amphibian and reptile habitats (with coloured maps of ecological provinces, sections, and subsections), natural vegetation of Minnesota, average precipitation, temperature, and a table of amphibian and reptile distributions by ecological section. Watersheds are discussed and mapped. A table presents amphibian and reptile distributions by habitat type. Aquatic habitats are lakes and ponds, marshes, prairie wetlands, and peatlands. Terrestrial habitats are flood-plain forest-coniferous-northern hardwood forest, and prairies. Disturbed areas are discussed separately as agricultural lands and urban and suburban habitats. Next come suggestions for observing and studying amphibians and amphibians and reptiles encompassing ethical field methods, field study and care of captives. A conservation section, divided between habitat loss and pollution is followed by amphibian declines, diseases, harvesting pressures, and persecution. Common amphibian and reptile problems covers snakes in house, garage, and yard invasions, salamanders in basements, turtles nesting in the yard, snapping turtles eating ducklings, and salamanders, frogs, on the road or yard.

A checklist gives the original describer(s), the year named for each genus, species and subspecies. Systematics and taxonomy follow Frost *et al.* 2006. Bulletin of the American Museum of Natural History, and English names follow Crother, *editor*, 2012, SSAR Herpetological Circular 39.

Species accounts are grouped by class and, within each, by family, each prefixed by summaries of features. Each individual species account starts with current English (common) and scientific name, and continues with description, and distribution in United States and Canada (but statements for the latter are vague and often omit actual extent apparently in an effort to be concise). A small map of Minnesota counties shows museum records indicated by half-filled (pre-1960) or solid (post-1960) circles and literature or sighting records as open circles. Habitat, and life history, and remarks (including legal status) complete each account.

Species of possible occurrence include mention of released exotics and abbreviated species accounts for three species that further field studies in the state may yet find. Concluding the book is a glossary giving definitions from amelanism to ventral, resources (references and organizations), literature cited, and index to genera, species and subspecies.

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Amphibians of Ohio

Edited by Ralph A. Pfingsten, Jeffrey G. Davis, Timothy O. Matson, Greg Lipps, Jr., Doug Wynn, and Brian J. Armitage. 2013. Bulletin New Series Volume 17, Number 1, Ohio Biological Survey, P.O. Box 21370, Columbus, OH, USA, 43221-0370. 916 pages, 90.00 USD, Cloth.

The US state of Ohio lies along the southwestern end of Lake Erie, between Pennsylvania on the east and Indiana on the west. It is adjacent on the north to the richest area (southwestern Ontario) for species of amphibians and reptiles in Canada. Ontario includes the most northern of the Lake Erie's western islands. It is therefore unsurprising that the accounts contained in this detailed review of Ohio amphibians which includes the islands to the south (as well as the mainland beyond) are very relevant to the interests of Canadian herpetologists, naturalists, and conservationists.

Publication on Ohio's amphibians and reptiles began early in the nineteenth century when they were included by Jared Porter Kirkland in his 1838 list cov-

ering the settled region west of the Appalachians at that time. Ohio frogs and toads were treated in detail by Charles F. Walker in 1946 based on field surveys he initiated with colleagues and students in the 1930s but a companion volume on salamanders did not appear until the multi-authored treatment edited by Ralph A. Pfingsten and Floyd L. Downs in 1989.

The growing attention on herpetological research after the Second World War was reflected by the initiation of the *Ohio Journal of Herpetology* in 1957 by the Ohio Herpetological Society. The journal was soon rechristened as the *Journal of Herpetology* and its publisher as The Society for the Study of Amphibians and Reptiles. This became a leading international research journal, joining the longer established *Copeia* (originating at the American Museum in New York in 1913 and later adopted as the publication of the American Society of Ichthyologists and Herpetologists) and *Herpetologica* begun in Kansas in 1936 which became the publication of the Herpetologists League. Despite its world coverage and influence, many of the society's members continued to focus their efforts, at least in part, on their native herpetofauna in Ohio.

The latest contribution of the latter and their supporters is a weighty volume by many measures, including sheer size (over 900 pages). This detailed treatise begins by presenting summaries of the influences on Ohio herpetofauna of its geology, soils, climate, habitats, and the integrated Ohio environment. Then there are sections on amphibian systematics (including diagnosis of families). The species accounts which follow are the major contribution. They begin with identification keys for all included species followed by individual coverage for each member of five families of salamanders (24 species, 13 of these occur in Canada) and four families of frogs and toads (14 species, 12 of which occur in Canada). A bonus account covers hybrid salamanders which are usually female and may be diploid, triploid or higher polyploids. These variously have genes from *laterale* combined with one or two of *jeffersonianum, tigrinum, texanum, and barbori*. Accounts cover etymology, synonyms, taxonomic status, common names, description, and all aspects of natural history. They also include photos of typical and variant metamorphosed juveniles and adults, salamander larvae and anuran tadpoles, eggs, drawings of key morphological and behavioural features, tables of measurements and photos of habitats. Together these set a new standard for regional coverage. They draw not only on herpetology research in the state but also studies beyond its borders wherever significant observations and data on species present in Ohio. The distribution of each species Ohio is presented on a vegetation base map with dots for only those county records that have vouchers (photographs or museum specimens).Three time periods are distinguished (before 1952, 1952-1989, and after 1989). A small inset map gives the whole North American range.

Final sections cover potential occurrences and exclusions, and practical applications of the data gathered for developing priorities for conservation of Ohio's amphibian diversity; amphibian conservation; Ohio amphibian distributions; environmental applications. Indicative of the comprehensiveness of this volume and therefore its value as a reference to the ever-growing number of productive researchers focussing on amphibians, is that the double-columned Literature Cited takes 73 pages.

Support for this publication reflects, like its multiple authorship, how effective group effort can be. Its development has been supported by the Ohio Division of Wildlife through its Wildlife Diversity and Endangered Species Fund, with additional assistance for printing from Cincinnati Zoo, the Cleveland Museum of Natural History, the Columbus Zoo and Aquarium, the Crane Hollow Foundation, the Toledo Zoo, the Akron Zoo and the Toledo Naturalists' Association.

In recent decades there has been a succession of new guides to other states, but this is by far more comprehensive and detailed than is usually attempted and raises the bar to a level that its successors will find hard to exceed or even match. All the many people contributing to the research, review, editing, and publication may be justly proud.

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Illustrated Checklist of the Birds of the World – Non Passerines

By Josep del Hoyo, Nigel Collar, David Christie, Andrew Elliott, and Lincoln Fishpool. 2014. Lynx Edicions, Montseny, 8, 08193 Bellaterra, Barcelona, Spain. 904 pages, 145.00 EUR, Cloth.

I am not a fanatic lister, but an observer who religiously keeps notes. When I retired I realised the last time I added up my life list was 40 years earlier. I decided it was time for an update. Using the Sibley and Monroe World List of Bird Names (1999) I tried five times over four years to complete this daunting task. There were many times when it was not clear which species I saw and I had to undertake much slow, research to resolve each issue.

Now we have a Lynx Edicions version of the world bird list. The authors take 54 pages to review and explain the process that lead them to declare one group of birds as a single species. The authors use the Biological Species Concept (BSC relies on defining repro-

ductively isolated populations) along with a scoring system that evaluates differences in morphology, song, ecology and geographical relationships. Using this process they have produced a volume that covers 4,372 extant species of non-passerines (Volume 2 – Passerines will be published in 2016). Also covered are 99 species that have become extinct since 1500, with 50 of them illustrated.

Each entry gives the currently accepted species in English. Then lists the names in French, German and Spanish, as well as alternative common names in English. There is a brief set of taxonomic notes to support the decision to accept species designation. All species have a distribution map and a colour illustrations, including distinctive subspecies where appropriate. (The artwork is high quality and mostly taken from the Handbook of Birds of the World series). The index is colour coded to show extant taxa, old or invalid taxa and extinct taxa – a useful idea. There are 34 maps and a full bibliography.

So how useful is this new book? My first thought was to check Hen Harrier. In Europe I had seen these birds hunting mice over upland heath. When I arrived in North America there was a raptor called a "Marsh Hawk." To me this was a different bird as it was a little grubby in appearance and I typically saw it hunting and catching frogs and snakes over wetlands. The bird's use of a stall-stopping dihedral was more pronounced. To my surprise this was the same species – *Circus cyaneus*. For 50 years I have waited for an authority to split these harriers in two. Del Hoya and his colleagues have finally taken this plunge.

My next challenge was to review the typical toucans. On every trip to South America I have had to research which species I have seen. Handbook of Birds of the World Volume [Josep del Hoyo, Andrew Elliott and Jordi Sargatal (2002), Lynx Edicions, Barcelona, Spain] listed 7 full species. Del Hoya now lists 11 species and it took me a couple of hours to evaluate whether my own notes were correct. (Wikipedia currently lists eight species with 6 sub-species). Where the taxonomy will settle I would hate to guess. At least the issue of whether the Red-billed Toucan (*Ramphastos tucanus*) and Cuvier's Toucan (*Ramphastos cuvieri*) should be considered species (they are significantly different in their bill colour) I am sure will rage on, because they interbreed freely.

Six years ago I saw and photographed a nightjar in central India. Originally I listed it as a Grey Nightjar (*Caprimulgus indicus*) and not an Indian Nightjar (*Caprimulgus asiaticus*). My 1999 field guide showed the Grey distributed India-wide. Back in Canada, when I reviewed my notes, I became confused. Handbook of Birds of the World Volume 5 [Josep del Hoyo, Andrew Elliott and Jordi Sargatal (1999), Lynx Edicions, Barcelona, Spain] contained a reference to *Caprimulgus indicus* as the widespread Jungle Nightjar. The Indian Nightjar (*Caprimulgus asiaticus*) had a similarly broad Indian distribution. Looking at my photo I finally decided my bird was an Indian Nightjar. This new book shows the Grey Nightjar (*Caprimulgus jotaka*) as having a very limited range in north-east India and the Indian Nightjar (*Caprimulgus asiaticus*) occurring throughout the Indian mainland. This confirms my sighting as an Indian Nightjar – doesn't it?

My other question was did I miss or misidentify Fork-tailed Swift among the large number of "Palm Swifts" I saw in Mongolia. This book lists Fork-tailed Swift as an alternative name of the Palm Swift subspecies. However one researcher has split this "superspecies" into Salim Ali's Swift, Blyth's Swift, Cook's Swift as well as Pacific Swift. This split has been accepted by the International Ornithological Committee (IOC), but not the International Union for Conservation of Nature, nor del Hoya *et al.* (but with five sub-species). For now I am sticking with Palm Swift and del Hoya.

The authors have changed some of the English names too. Why list Peregrine as invalid and replace it with Peregrine Falcon? They retain the old English names of Merlin, Kestrel, Hobby etc. but change Peregrine and Gyr. (To be consistent it should be Merlin Falcon etc.). Original texts do not have this modification (especially as "falcon" is the term for female only). They have also "updated" names like Fea's Petrel (to Cape Verde Petrel). This could be confused with the Cape Verde Storm Petrel (*Oceanodroma jabejabe*) which is now regarded as a separate species by the British Birding Association and others, but not by del Hoya *et al.* Oh, the joys of taxonomy!

So is this book really useful? Without question it is. It is now the most current and up-to-date checklist of world birds. It has been assembled by people who have spent over twenty years evaluating and deciding the taxonomic issues related to birds. It is a complete checklist of the non-passerine species using the most up-to-date taxonomy. Having both an illustration and a range map alongside of the species entry is a real blessing. It is an essential purchase for researchers and for all those engaged in world-wide birdwatching. Even if you are not a combat lister, you still need to know which species you have seen and where. It will now be my go-to text. There is one critical question. Will Volume 1 be out-of-date before they publish Volume 2?

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Life on the Rocks: A Portrait of the American Mountain Goat

By Bruce L. Smith. 2014. University Press of Colorado, 5589 Arapahoe Ave., Suite 206C, Boulder, CO, USA, 80303. 192 pages, 35.00 USD, Cloth. (Also available as an e-book)

Anyone who has ever done any rock climbing or scrambling is likely in complete awe of the feats that mountain goats manage in the steep terrain that is their home year around. The photos in this book attest to their ability to survive "life on the rocks," and the text helps the reader understand how they do it, physically and physiologically.

While *Life on the Rocks* could be described as a "coffee table book" by virtue of its size (31 cm tall × 24 cm wide) and plethora of colour photographs (over 100, the majority taken by the author), to limit it to that category would do both the book and the author, a disservice. Smith is a scientist with the US Fish & Wildlife Service, and the photographs complement his well-written text on the mountain goat's taxonomy, anatomy, behaviour, environment and co-inhabitors of extreme terrain, rather than the text just being an expanded caption for each photograph. As well as life history and natural history (Part I), Smith discusses current population estimates and reasons for declining numbers, and the conservation challenges that impact mountain goats (Part II). And, throughout the book Smith weaves in tales of his personal adventures as a field biologist studying mountain goats, particularly in the Selway-Bitterroot Wilderness of southwestern Montana.

The majority of the photographs are excellent, and range from intimate portraits to broad landscape images. The quality of some of the full-page images do suffer from apparently having been scanned from decades-old slides or colour prints (e.g., the landscape photo on page 109), although these are often used to illustrate a point or theme, for which they are adequate. (As an aside, it would be interesting to know if the photographs reproduce more sharply in the Kindle e-edition.) Many photographs are reproduced in two-page spreads, some of which are truly outstanding, such as the backlit goat (including breath vapours) on pages 134–135, also used on the book's cover jacket, or the close-up of a pika with a mouthful of vegetation (pages 160–161). Smith includes many photographs of other species that share the mountain goat's environment, which help to illustrate his text. I did notice an error on photo pages 148–149, where the caption refers to whitebark pine dying from disease and insects, whereas the photo clearly depicts lodgepole pine and subalpine fir, whose red needles are likely the result of the phenomenon known as "red belt," where a temperature inversion causes the tree's needles to transpire, while the roots are still in frozen ground and unable to take up moisture, causing desiccation of the needles.

It would have been useful to have had the sketches of different ages and sexes of mountain goats near the beginning of the book, rather than near the end, so that the reader could refer to them when looking at some of the photographs. Smith highlights pertinent research in an easy manner throughout the book, but while there is a page of suggested references (including scientific papers), I would have liked source notes for some of the chapters, relating his statements to specific research papers.

Relatively early in the book Smith states that "at its core, the goat is both product and captive of its evolutionary history and specialization as a mountain climber." This could also be an introductory statement for the chapters on local and global conservation challenges. While wildlife and land managers can reduce harvest levels and minimise human disturbance, only a landscape approach will ensure that mountain goats survive in a world with a changing climate. Smith touches on the uncertainty of how mountain goats may respond: their generalist diet may help them cope with vegetation changes, but they are intolerant of summer heat so where will they go when the temperature rises, and what might changes in parasite loads and transmission vectors mean for the goat? As such questions are just starting to be asked of mountain goats, Smith refers to research involving other inhabitants of these mountain ranges, such as pika.

If you've ever looked up at a mountain goat on a seemingly impossible ledge and wondered how come it doesn't fall off that cliff or what does it eat in winter? And how does it stay warm? then you will enjoy this book and its many photos.

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The Fish in the Forest: Salmon and the Web of Life

By Dale Stokes, Photographs by Doc White. 2014. University of California Press, (California-Princeton Fulfillment Services), 1445 Lower Ferry Road, Ewing, NJ, USA, 08618. 159 pages, 29.95 USD, Cloth.

"The story of the Salmon Forest is a story of the interconnectedness of the sea and land and a fish that has evolved and become entwined in a landscape, a story that serves as a metaphor for all of life on earth."

These lines set the tone for Dale Stokes' book on the natural history of salmon and their environment in the north Pacific. In just under 150 pages, Stokes describes in careful detail how the 'King of Fish' is an important ecosystem engineer in the forests of the north Pacific, particularly the coasts of British Columbia and Alaska. He does so with a tangible passion that sometimes edges into reverence – Stokes clearly loves this fish, and uses this book to tell us why we should too. *The Fish in the Forest* is not short on scientific terminology – we're treated to a whole host of Latin species names and biological details. But Stokes' obvious excitement for the subject saves it from being a dry textbook – it feels more like listening to a passionate teacher lecture on his favourite topic, for example: "Taken from the Latin, *semelparous* means 'begotten once,' a reference to their lyrical existence: they die soon after they reproduce."

Stokes routinely sees the poetic in everything, which can get a little grating at times and overly anthropomorphic. Female salmon sound heroic when he describes the final stages of their life cycle: they "invest their last metabolic energy in egg production and in guarding their nests until they become too weak and battered to hold their position in the current, and they drift away to die." All technically true, but the language almost makes the salmon sound like martyrs – not the most apt analogy, as fish do not have the power of free will. Still, Stokes' writing style makes for a very enjoyable and informative read. The full colour photographs by Doc White are definitely assets – my favourites are the underwater shots of glistening salmon. White's photos bring to life the whole Salmon Forest, from delicate riparian vegetation to ancient cedars towering over gravely creeks, and powerful apex predators to gelatinous fish eggs.

Stokes begins this story by precisely defining key terms and addressing basic questions: What is a fish, a salmon, the Salmon Forest? For the most part, all fish are aquatic, poikilothermic (a fluctuating internal body temperature) vertebrates with gills. There are five species of salmon that frequent the Pacific Northwest: large Chinook (up to 50 kg); vibrantly striped Chum or Dog; small and abundant Pink; Coho or Silver, which spend the most amount of time in freshwater; Sockeye, the 'fish of fishes', with the longest spawning run and the ability to battle raging rapids head on, and the fresh water variant Kokanee, which live their entire life cycle in landlocked streams and lakes. The Salmon Forest is defined geographically as the coastal forests from northern California through to British Columbia and Alaska, and across the Pacific to Russia, Japan and Korea.

In chapter 2 we learn about the life cycle of the salmon, and the biological traits that set these fish apart and contribute to their special role in the forest. Two of the defining traits of salmon are semelparity and anadromy. Semelparous organisms die after one reproductive cycle, and invest all of their metabolic energy into the survival of their offspring. Anadromous fish migrate upstream to spawn, either from marine to freshwater environments, or further upstream if they are exclusively freshwater species. In salmon, this ensures that valuable marine nutrients are brought into the forest systems surrounding freshwater streams. These really are fascinating fish – their ability to return to their natal streams is particularly incredible, and it's believed that tiny particles of magnetite in their skulls act as a sort of compass to guide them home, in a process called olfactory homing – not dissimilar to the experiences of migrating birds.

In chapter 3 we learn about how the very small – the isotope signatures in salmon flesh – impact the environment in a large way, leaving their mark throughout the entire forest ecosystem. Since the development of the mass spectrometer, scientists are able to trace a species' isotope signature through the environment. In this case, salmon flesh leaves a distinct trace of marine-derived nutrients, which has been found throughout the Salmon Forest, from the needles of giant cedars to the bones of coyotes.

Entitled 'Salmon Gestalt', chapter 4 covers several concepts of ecological study, including the niche theory, trophic levels, food webs and keystone species. At first it seemed unnecessary to discuss the history of ecology, but by the end of the chapter it was interesting to see how Stokes linked the study of salmon to the study of all life.

After defining the salmon and how we might see its signature throughout the Salmon Forest, Stokes uses chapter 5 to look at the natural history of the diverse flora and fauna that call this ecosystem home. Of particular interest are the examples of plant and insect phenology that are tightly linked with the salmon life cycle, such as the case of the blowfly and kneeling angelica (*Angelica genuflexa*). The riparian angelica blooms approximately ten days after salmon spawning begins, when adult blowfly are around to pollinate their flowers. After feeding on the blooms, the blowflies lay their eggs in the recently spawned salmon carcasses. Stokes demonstrates how the forest is dependent on an indescribably complex series of relationships between predator and prey, biogeochemical cycles and biotic/abiotic

interactions. There is simply no way to understand the whole by prying apart the individual threads.

The concluding chapter brings us full circle, and discusses the role of salmon as ecosystem engineers, inevitably leaving their mark on every aspect of the forest landscape in the Pacific Northwest, including the people that call the region home. Although Stokes does not go into great detail about recent ecosystem destruction, it is certainly implied that although resilient, these species and this environment are nonetheless vulnerable to our rapacious appetites for salmon, and our unfortunate habit for resource exploitation. It's almost impossible to quantify the importance of a keystone species like the salmon, but according to Stokes, "if we truly valued the intrinsic worth of the salmon as a part of the Salmon Forest, perhaps we'd realize that we can't afford to exploit them – and we wouldn't want to."

I would certainly recommend this book to anyone interested in natural history, and the beauty of the intricate connections between a fish and its forest.

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Biology and Conservation of North American Tortoises

Edited by David C. Rostal, Earl D. McCoy, and Henry R. Mushinsky. 2014. The Johns Hopkins University Press, 2715 North Charles Street, Baltimore, MD, USA, 21218-4363. 190 pages, 69.95 USD, Cloth.

The North American tortoises, or gopher tortoises, are known for their digging ability. Most of the species dig extensive burrows for shelter. These tortoises are limited to the southern parts of the United States, from California to Florida, as well as parts of Mexico, but all of them face significant conservation challenges.

This book consists of 18 chapters on various aspects of the biology and conservation of North American tortoises. None of the chapters focus on individual species. Instead, each chapter addresses what is known about a topic for all of the species. Chapter topics include the fossil record, systematics, thermo-regulation, reproduction, growth, health issues, habitat, movement patterns, genetics and conservation. Over half of the chapters have multiple authors, usually with experts on different species collaborating on a topic.

It is difficult to name the five species covered in this book, as the 33 authors could not agree on either the common or scientific names. Until recently there were four accepted species in one genus. The western Desert Tortoise was split into two species, and it is possible that further genetic analyses will reveal more species within the group. Most of the authors of this volume consider all of the North American tortoises to be in the genus *Gopherus*, but a few consider that three of the species should be placed in a different genus, *Xerobates*. Common names are also contentious. The two Desert Tortoises are commonly referred to as the Mohave (or Mojave) Desert Tortoise and the Sonoran Desert Tortoise but some herpetologists object to these names, preferring Agassizi's and Morafka's Desert Tortoises.

Overall, these chapters provide a thorough overview of the biology of North American tortoises, including research published up to the year 2012. For the most part the chapters just summarize the scientific literature on the five species, but a few chapters provide additional analysis of existing data. Some of the chapters are vague on some topics. Climate change is mentioned as likely resulting in more droughts which would likely affect many of these species, but there is no attempt to quantify such statements. Drought certainly is a significant threat to tortoises as individuals can lose 40% of their body weight during a severe drought. Longer or more frequent droughts as a result of climate change could lead to desertification and local extinctions.

Other threats are more clearly addressed. Invasive exotic grasses are a significant issue in many western areas, but since tortoises will eat both grasses and forbs, it might be thought that exotic grasses pose little threat to the tortoises. Forbs, however, are more nutritious than grasses, so if plant communities become more grass dominated this could be a serious threat to the tortoises. In addition, many exotic grasses promote severe wildfires that can kill tortoises.

The final chapter of the book provides a detailed overview of the threats and conservation needs of these tortoises. Despite protection of some populations dating back over 20 years, all these species are still declining. The Bolson Tortoise, limited to a small area of northern Mexico, has even been listed as one of the top 40 turtles or tortoises at risk of extinction. And new threats continue to emerge. For example, fracking potentially affects nearly 50% of the range of Berlandier's Tortoise in Texas. Not surprisingly then, the major issues facing these species are adequate protection of populations and their habitat. This book successfully summarizes the state of knowledge about North American tortoises, but it is hard to be optimistic for the future of these species.

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Societies of Wolves and Free-ranging Dogs

By Stephen Spotte. 2012. Cambridge University Press, New York, NY, USA. 394 pages, 58.00 USD, Paper and Kindle. 133.00 USD, Cloth.

Stephen Spotte's book, *Societies of Wolves and Free-ranging Dogs*, is a detailed account of wild wolves and free-ranging dogs (including dingoes) living throughout the world. It is well researched with 73 pages of endnotes, 50 pages of references, and a 16 page index. The volume is 394 pages but ends on page 238 before the citations noted above, and after 16 pages of Roman numeral introductory material. The jacket cover of the book accurately summarizes its contents: "Wolves are charismatic emblems of wilderness. Dogs, which descended from wolves, are models of urbanity. Do free-ranging dogs revert to pack living or are their societies only reminiscent of a wolfish heritage? Focusing on behavioral ecology, this is the first book to assess societies of both gray wolves and domestic dogs living as urban strays and in the feral state. It provides a comprehensive review of wolf genetics, particularly of New World wolves and their mixture of wolf, coyote and dog genomes. Spotte draws on the latest scientific findings across the specialized fields of genetics, sensory biology, reproductive physiology, space use, foraging ecology and socialization. This interdisciplinary approach provides a solid foundation for a startling and original comparison of the social lives of wolves and free-ranging dogs."

I am not sure if the manuscript is a startling comparison of wolves and dogs but it is certainly original in how it combines the two canines into one volume. I found it very odd though that Spotte, a well published marine biologist, would write such a detailed book on the Canidae family, considering that he does not appear to have any prior publications on the topic and only cites one of his previous references (on zoos) in this book. That is not a negative comment, but rather more of a curiosity on my part. However, I would have at least liked for Spotte to have explained his decision to write such a treatise, even if briefly discussed. He certainly wrote the book with a different perspective than a full-time canid biologist, as I'll explain below.

I already have a fair bit of information (e.g., books, scientific papers, personal research) on wolves and coyotes, so in reading *Societies of Wolves and Free-ranging Dogs* I learned more about dogs, both free-ranging ferals and dingoes, than I previously had knowledge of, and will likely use this book as a reference on them. I found it useful to have behavioural information on city strays and feral dogs and to learn about dingo ethology which seems to be dramatically different than wolves and more of a mix of dog and wolf, including their reproductive cycle and ecology such as not living in packs and displaying questionable parental care of offspring. However, it was pretty clear that there isn't nearly as much scientific information published on dingoes and feral dogs as there is on wolves, especially considering that most of the dingo literature that was referenced was dated and much of that was anecdotal (e.g., second hand reports of 1 2 sentences on some aspect of dingo ecology such as parental care).

The book is a literal encyclopaedia of information on what makes a wolf, what makes a dog, visual and tactile communication, olfactory and vocal communication, space, foraging, courtship and conception, reproduction and parenting, and socialization. Spotte did a commendable job of synthesizing knowledge on both wolves and dogs which is an enormous task. I did find many sections that were very "heavy" and lengthy to read; for instance, the introduction to chapters, such as Chapters 3.1 (p. 33–38) on metaphors and semiotics and 4.1 (p. 61–66) on odour and pheromone reception, were especially time consuming and philosophical despite being information filled. Thus, the book was more of a reference book than something to sit down and casually read. I found that it took me multiple hours to comprehend each of the 9 chapters and, as the author suggested on p. xii, I had a bookmark in the endnotes and reference sections. While I tried to simply peruse through the book I found the scientist in me constantly paging to the endnotes and then to the references to find the quoted works. This took me considerable time bearing in mind that each chapter had between 170–474 endnote citations. And herein lies my intrigue with the book: Spotte cites many references (50 pages) but relies disproportionately on older studies from the 1940s-1970s. While many of these volumes are seminal studies, such as Adolph Murie's (1944) *The Wolves of Mount McKinley*, Ian Cowan's (1947) *The Timber Wolf in the Rocky Mountain National Parks of Canada*, Lois Crisler's (1958) *Arctic Wild*, and Dave Mech's (1970) *The Wolf*, I thought that the author cited them way too much, especially considering the hundreds of new manuscripts which are more up-to-date and comprehensive such as Dave Mech and Luigi Boitani's (2003) *Wolves: Behavior, Ecology, and Conservation* which was cited much less frequently. However, to have 73 pages of endnotes is a massive undertaking and there are newer references mixed into those older works making the book certainly usable and for the most part current.

I found Spotte's perspective very interesting even if I disagreed with some of his premises such as his suggestion to name red wolves as "red coyotes" (p. 8), calling Great Lakes wolves the same as eastern wolves (page 7 note: most of the literature separates the two as Great Lakes wolves are believed to be eastern wolf × gray wolf hybrids), and his behaviorist viewpoint and repeated mention of animals unable to recognize the mental state of others (page 74) or that non-humans do not possess a theory of mind (page 34). My guess is that

Marc Bekoff, and many other scientists that study animal cognition, would disagree with this perspective. While Spotte casts doubt if admixed canids deserve species status (p. 5), I disagree as new research is informing us that hybridization is a natural process and the cause of rapid evolution in many groups of animals, such as canids in eastern North America, most notably the eastern coyote/coywolf (Canadian Field-Naturalist, 2013, 127: 1–16).

Despite my comments noted above, I do endorse the book as it is a valuable reference for anyone's book shelf and it provides a very well synthesized version of both wolves and dogs. However, the following are my four major criticisms of the book:

The first is simply the expense of book. When I looked at the price on Amazon.com I was stunned how expensive this simple soft-cover, nearly 400 page book was. In fact, the *sale* price for the Kindle edition was 36.80 USD, and 52.20 USD for paperback, and 110.44-126.35 USD for the hardcover version. I don't understand why the book is so expensive especially since it is black and white and could be printed on demand for significantly cheaper than that. The price alone makes it difficult to justify purchasing except maybe for an upper level college or graduate course.

Second and bizarrely, the book (page 238) just ends after the dingo socialization section of Chapter 9 with no conclusion whatsoever. I strongly believe there should have been a Chapter 10 that synthesized the information that I digested in the first 9 sections. Without this summary the reader is left wondering what the main take home messages of the book are.

Third, Spotte is a tad critical of previous studies and theories and is inconsistent with his criticisms. I think this may have a bit to do with the author not having a background studying canids even if he has a strong scientific understanding. There were many sections of the book that I just didn't feel right with but sometimes couldn't place my finger on exactly why I felt that way because I was trying to trudge through all of the information (this would probably be similar to me writing a detailed book on marine mammals and then having a marine biologist review it). For instance, on page 67 Spotte claims that wolf scent marking as a territorial boundary is more anecdote than empirical yet he then repeatedly makes claims and references in the endnotes (especially some of the older citations noted above) supporting such behavior. I found it difficult to go back and forth from the chapter to the endnotes when reading these types of passages, especially where there is much scientific agreement on a given topic like canid territoriality and scent marking. In other words, the author is critical of the scientific literature in many sections (using philosophical arguments of why things like territoriality aren't proven) yet he then attributes many of his statements with older citations that may even be anecdotes themselves (like the books published in the 1930s-1950s).

And fourth, the book is repetitive in many sections, but this isn't a major complaint. While this may be expected of a major work I found the frequent references to go back to a specific chapter, reference, or endnote frustrating. But that was most likely because I was reading the book from cover-to-cover instead of using it as an encyclopedia-like reference whereby that repetition may be useful to the reader.

Despite some of my issues with *Societies of Wolves and Free-ranging Dogs* it is certainly a unique reference on wolves and dogs, which are now generally regarded as the same species. In one book, it synthesizes what is known on the most recognizable of all canids and I don't think that has been done before. Thus, despite me disagreeing with certain sections and viewpoints, I would recommend the book as a reference for canid enthusiasts if one can afford the price. However, the book is not for beginners on the subject matter of wolf and dog ecology and behavior as it is a time-consuming and exhaustive read.

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BOTANY

Plantes de milieux humides et de bord de mer du Québec et des Maritimes

By Martine Lapointe, Michel Leboeuf, and Arold Lavoie. 2014. Guides nature Quintin, 4770, rue Foster, Waterloo, QC, Canada, J0E 2N0. 455 pages, 34.95 CAD, Cloth.

This latest edition in the Michel Quintin nature guides is a visually pleasing publication having numerous colour photos of plants and of wetland habitats, crisp line drawings and illustrative graphics. It covers 302 species of flowering plants, ferns, horsetails, club-mosses as well as hepatics and mosses. The guide is stated as being aimed at nature lovers as well as specialists undertaking wetland and seashore plant inventories within Quebec and the Maritimes. However, it is likely better considered as a good introductory guide to the flora and vegetation of these habitats for avid naturalists and students of ecology. Anyone engaged in a comprehensive documentation of the vegetation of wetland habitats would, by necessity, require a more detailed floristic reference work. This would certainly be the case to differentiate morphologically similar species in the more difficult groups such as the sedges, grasses, and rushes common in these habitats.

The initial section of the guide provides an excellent introduction to wetland types and their relationship to water levels and vegetation present through the use of illustrative graphics and photos. A very helpful feature of the guide is the listing of locations of representative examples of wetland habitats, along with colour photos, of specific marshes, swamps, bogs and various types of seashore habitats. The introduction to flowering plants provides an oversight of the diversity found in vegetative and floral structures through drawings that illustrate the range in leaf types and form and of inflorescence structure. These illustrated glossaries aid the non-specialist in understanding the technical descriptive terminology used in the guide. At the same time, it permits the author to provide more precise descriptions of plant form within the individual species treatments.

The species covered are grouped into seven categories readily identified by the colour coding on a portion of the unbound side and corner of the guide: trees and shrubs; terrestrial plants; aquatic plants; maritime plants (wet habitats, dry habitats); sedges and members of the sedge family, as well as grasses and rushes; ferns, horsetails, and clubmosses; hepatics and mosses. The identification of species is based initially on the placement of a plant in question into one of the seven categories. Subsequent identification to species is based in large part on a comparison of vegetative and floral structures exemplified in the colour photos and line drawings. For herbs and some shrubs with distinctive flowers or flower clusters, a colour gallery of flowers, grouped by colour, is provided for 155 species as an identification aid. Within difficult groups of flowering plants, such as the sedges, grasses, and rushes, an introductory set of colour graphics help differentiate these groups. Similarly for ferns and allies and the hepatics and mosses, graphics of their growth form and structures are provided.

Each individual species treatment includes several elements. The visual portion includes a colour photo with the main distinguishing features of the plant accompanied by a line drawing with details of appropriate vegetative and floral/fruiting structures. Colour inserts of floral or vegetative details within the larger plant images of some species are not always helpful due to their small size. Additional visual aids are provided by symbols that provide further information on the biology or usefulness of the plant: whether the plants are obligate or facultative wetland species; light requirements; longevity (perennial, biennial, or annual); use in re-vegetation of riparian banks, and whether the plants are invasive.

The main descriptive texts include the French common name in bold typeface followed by the scientific name, English common name and the family name. Organization of the species within each section is alphabetical by the French common name. Descriptive texts for each species cover such aspects as size and habit, branching/bark/leaves, flowers, fruits, habitat and distributional range. Sections on similar species or notes on such aspects as toxicity or uses are also provided. In the texts for ferns and allies and for hepatics and mosses, information on their distinctive reproductive structures is provided.

The characteristics of each wetland species of southern Quebec, treated in the guide, are summarized in a table organized alphabetically by scientific name following the species treatments. The table summarizes and codifies species on such aspects as whether they are obligate or facultative wetland species, and for those obligates, whether they are species always found rooted in water or whether they are true aquatics, partially or totally submerged. The species are further identified as to their growth form (e.g., tree, shrub, herb) or type of aquatic (emergent, submerged etc.), and spatial placement within the littoral zone. Each species is also assessed as to its level of threat and whether it is an invasive exotic or if useful for revegetation purposes. The table is perhaps most useful to students of wetland ecology, with the information on level of threat (threatened, vulnerable or possibly at risk of decline) being of more general interest to naturalists. A glossary of terminology, a bibliography, a list of useful internet sites, credits, and an index to species complete the guide.

The guide is a very pleasing and useful tome for gaining a basic understanding of the plants and vegetation of wetlands. Its appeal is based to a large extent on the high quality of the paper, illustrations, and photos, the informative graphics on wetland composition, the useful explanatory texts, and concise technical species treatments. It is a relatively hefty guide (about 0.8kg) for its modest size of 13 by 20 cm. Because of this, it might be best used as a reference tool at the roadside while exploring habitats referenced in the guide, rather than as a pocket field guide, carried along while slogging through a wetland.

ERICH HABER

60 Baywood Drive, Stittsville, ON, Canada, K2S 2H5

Trees of Eastern North America

By Gil Nelson, Christopher J. Earle, and Richard Spellenberg. 2014. Princeton University Press, 41 William Street, Princeton, NJ, USA, 08540-5237. 720 pages, 29.95 USD, Paper.

There are several field guides available for eastern North American trees. One of the more recent is the Sibley guide (Sibley 2009), the National Wildlife Federation field guide (Kershner *et al.* 2008), and the Peterson guide (Petrides 1988). The Petrides (1988) guide covers roughly the same geographic area as this guide whereas the other two are US and Canada. Nelson and Spellenberg are also listed as authors of the Kershner *et al.* (2008) guide.

Back to the Nelson *et al.* guide that is the subject of this review. This guide which is a hefty 720 pages, covers virtually all species of tree expected to be found in the eastern part of North America which is roughly defined as the Northwest Territories/Nunavut boundary and a line extending southward and slightly east of the Manitoba/Saskatchewan border continuing southward along or near the 100th meridian until it enters Texas. In Texas the line traces along the eastern edge of the Edwards Plateau to Austin and then south ending at the Gulf of Mexico at Corpus Christi. In contrast, the Peterson guide (Petrides 1988) considers all of the trees east of the Black Hills and Rocky Mountains. Thus, coverage is a bit different.

The present guide includes virtually all trees that "grow without the aid of human cultivation" (page 7) within the above-described area. This includes a number of exotic species that have escaped cultivation, which is a lot of species considering the guide encompasses all of Florida where many exotics have been planted as ornamentals. Also, because it includes a portion of south Texas, species of a more southwestern distribution are included. This species coverage is very similar to the Sibley (2009) guide except that Sibley includes many ornamental trees that are not at present known to naturally reproduce independent of human cultivation.

Of the alternative guides mentioned, this guide has up-to-date classification, and is reasonably compact so that it can be used as a field guide. The Sibley (2009) guide is not of a convenient size to carry on field trips. The quality of illustrations is far better than the other guides mentioned so that identification is easier. This includes the distribution maps which are sized to be clear. The text is error-free and no other editorial issues were noted while reading.

This guide can be recommended for each of the above reasons. It adds a very favorable choice to the selection of eastern tree guides presently available and is mid-way in price among each of the guides mentioned in this review. If you wish a new guide, an alternative guide to supplement others, or an off-the-shelf tree reference, I recommend this book for that purpose. I would also not hesitate to use this guide as a text for identification in a course of dendrology or any class involving plant identification. Foresters, horticulturists, wildlife managers, and other professionals will also find it usable. It adds to the many high-quality field guides now being published by Princeton University Press.

Literature Cited

Kershner, B., D. Mathews, G. Nelson, R. Spellenberg, T. Purinton, A. Block, G. Moore, and **J. W. Thieret.** 2008. Field guide to trees of North America. New York, NY, Sterling.

Petrides, G. A. 1988. A field guide to eastern trees. New York, NY, Houghton Mifflin.

Sibley, D. A. 2009. The Sibley guide to trees. New York, NY, Knopf.

ROGER D. APPLEGATE

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OTHER

The Real Weed Man: Portrait of Canadian Botanist Gerald A. Mulligan

By Julie Mulligan. 2014. Published by Julie Mulligan, P.O. Box 304, Russell, ON, Canada, K4R 1E1. 238 pages, Paperback edition 16.84 CAN, Kindle edition 2.95 CAN (Amazon.com).

The Real Weed Man is a daughter's very personal account of her father's life and career at the Central Experimental Farm (CEF) in Ottawa. It is based on discussions with her father, family members, colleagues, and on entries from Gerry's daily diary begun in 1974, which are frequently quoted. Within the book's 25 chapters, beginning with the early years growing up in Ottawa, the author traces Gerry's association with the "Farm" over a period covering more than 70 years. Gerry followed in the footsteps of other family members of earlier generations who worked at CEF. He began as a summer student, then as a technician after High School, and subsequently, following the completion of his Bachelor of Science degree in 1952 from Macdonald College of McGill University, he was hired as a biologist. Through considerable perseverance and his abilities as a researcher and manager, Gerry rose through the ranks to reach the top level of the Research Scientist classification. Gerry eventually also served as the Director of the Biosystematic Research Institute at CEF from 1978 to 1987.

The author touches on many facets of Gerry's personality and career. We learn that Gerry is an avid sports, and especially hockey, fan, a devoted father and

husband, as well as a gifted researcher and manager. Gerry is a very disciplined individual and persistent in achieving his goals. He has always tried to be ethical in his approach to decision-making as a manager and was open to heading in new directions when so required. The biographical sketch deals not only with aspects of Gerry's personal traits, but also reveals, over a series of chapters, how he dealt with or views specific issues, either as a researcher or as a manager. These include such topics as health and safety in the workplace, annual staff appraisals, French in the public service, and genetically modified plants, among others.

Readers who are familiar with Ottawa, would be interested in the details on historical land ownership by the Mulligan family within the city and at CEF. Changes that have occurred over the years at CEF, in the focus of its operations and in staffing, are touched on as well.

The most surprising aspect of the book is the frankness of revelations on Gerry's interactions with colleagues and managers, or of his views about the published works of others specifically named in the book. Because of such anecdotes, the book would be of particular interest to many botanists and biologists.

The primary subject of the book is that of a botanist, a weed specialist, Gerald Alfred Mulligan, his strengths and possible weaknesses, his lifestyle and views. In this regard, I have some minor quibbles on content. The author tends to expand topics such as Gerry's lifelong stuttering into a long, personal and family account. This, for the reviewer, digresses too far from its relevance to Gerry's condition and its impact on his career. Similar, perhaps excessive tangents, dealing with family outings and incidents, related specifically to the author and her siblings, are included rather than remaining focused on Gerry's fieldwork activities. The chapter on photography might have been better treated under a different subject heading. Much of it highlights problems in maintaining a web site on Weeds of Canada rather than on Gerry's photography. The author also regularly inserts lengthy personal views rather than reflecting those of her subject.

Considering that this biography is likely of greatest general interest to botanists and biologists, the detailed definitions and discussion of botanical "type" collections seem unnecessary. It is unfortunate that the error in naming of the Gray Herbarium of Harvard University (GH), given as the "Great Herbarium of Harvard University" (page 50 and in footnote page 199), was not recognized. Similarly, the institutional citation for the herbarium known by its acronym CAN is given as " Canadian National Museum herbarium" rather than as "Canadian Museum of Nature". The updated names of institutions and the acronyms of their herbaria are readily found on the internet by searching on Index Herbariorum.

In spite of the above critique, the book is an interesting read. It provides a very detailed perspective of a Canadian botanist who is known widely for his work on the mustard family, his numerous plant chromosome counts and his documentation of the weeds of Canada. Gerry's life-time work and achievements were recognized by the Canadian Botanical Association in 2006 when it presented him with its prestigious George Lawson Medal "...for excellence in the contribution of an individual to Canadian botany".

ERICH HABER

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The Once and Future World: Nature as it was, as it is, as it could be

By J. B. MacKinnon. 2013. Random House Canada, One Toronto Street, Unit 300, Toronto, ON, Canada, M5C 2V6. 256 pages, 29.95 CAD, Cloth.

The Once and Future World by J. B. MacKinnon, co-author of *The 100-Mile Diet: A Year of Local Eating,* is an eloquent and thought-provoking exploration of nature and our place in it. It addresses the roles humans play within the natural world, the influence we exert on its complex systems, and the relationships we develop with our natural surroundings. It really is a book about *Homo sapiens* in nature.

The book is also an invitation. MacKinnon invites us to stretch our thinking and our imaginations beyond common knowledge to envision a different world and future. He does so by blending personal narrative, scientific fact, historical discovery, recent events, case studies, speculation about the future, and sweeping questions that trigger reflection on where we are today and what we would like the world, and the place of humans in it, to look like. Along the way, McKinnon discusses a wide range of concepts, including the anthropocene, change blindness, shifting baselines, cascade effects, ecosystem services, relaxed selection, progress trap, double extinction, re-wilding, habitecture, and more.

"Nature is a confounding thing" he writes in the first chapter (page 8), illustrating throughout the book how our relationship with and within nature is equally perplexing. He offers particularly intriguing perspectives on the past – a past which is itself confounding and imperfect, filled with drama, story, extinction, human 'progress', forgetting and denial, resulting in what he calls a "10 percent world" offering only one-tenth of its former natural abundance. Accompanying the impoverishment of natural abundance is the loss of relation-

ships, knowledge and cultural practices relating to the natural world – a loss of nature from human social networks, as he puts it.

Yet this loss and gradual impoverishment was not a deliberate trajectory, but rather an incremental "taking" from the environment by different arrangements of people in different places at different points in history. All these 'takings', McKinnon adds, occurred with limited approval to degrade the environment, and subsequent adaptation to the consequences. Now, after many millennia, the accumulated impact of the consequences and adaptations is becoming increasingly clear.

Yet it is still a beautiful world, as the title of Chapter 5 suggests, and nature has a life and a vitality all its own – "always expressing itself in a weed poking up from a crack in the concrete" (page 9) – which shows us a way forward despite challenges which appear overwhelming. McKinnon identifies one major challenge as a lack of awareness regarding the natural world which surrounds us – from weeds in sidewalk cracks, to birds of prey hunting in urban parks, to ocean life returning to the waters of a popular beach after the holiday season. The nature we surround ourselves with shapes us as a species, he points out, adding that we tend to prefer wilder, more diverse environments. In that light, an important and overlooked result of conservation and ecological restoration efforts may be the recovery of a certain wildness within ourselves. In the context, furthermore, of challenges and limitations faced by nature conservation and ecological restoration – in world where, as McKinnon points out, many people spend more time in virtual landscapes than natural ones – this 'human re-wilding' of sorts, and deliberate reconnection and cohabitation with wild species, may be more important that we realize.

McKinnon offers examples of human-nature reconnection and co-existence from different parts of the world. He devotes most of the entire last chapter of the book (excluding the epilogue), to an imaginary example illustrating how humans can live in a wilder world. McKinnon ends that chapter, and essentially the book, in echo of an earlier passage where he encourages us to "remember what nature can be; reconnect with it as something meaningful in our lives; and start to remake a wilder world" (page 157). He ends the book on a tremendously positive note, pointing out that "it just might be possible for seven billion people – maybe even more – to survive on this planet, and not only to stop the endless decline of the natural world but watch it return to astounding, perpetual life. All it will take is a wilder way of being human" (page 215).

It is difficult to do *The Once and Future World* justice in a book review. This rich, informative and optimistic book defies categorization and description. Let me just say that I recommend it highly for being well-researched, well-written, thought-provoking, imaginative, and compelling. May it compel readers toward a wilder future where, as McKinnon puts it, humanity can express its genius, and so can nature.

RENATE SANDER-REGIER

3, 11th Line, Bristol, QC, Canada

NEW TITLES

Prepared by Roy John

† Available for review * Assigned
Currency Codes – CAD Canadian Dollars, USD U.S. Dollars, EUR Euros, AUD Australian Dollars.

ZOOLOGY

* **Field Guide to the Birds of Australia – A Photographic Guide.** By Iain Campbell, Sam Woods, and Nick Leseberg. 2014. Princeton University Press, 41 William Street, Princeton, NJ, USA, 08540-523. 392 pages, 35.00 USD, Paper.

Birds of a Feather. By C. Rees, and D. Thomas. 2014. Troubador Publishing Ltd, 9 Priory Business Park, Kibworth, Leicester, UK, LE8 0RX. 200 pages, 12.99 GBP, Paper.

The Carnivore Way – Coexisting with and Conserving North America's Predators. By Cristina Eisenberg. 2014. Island Press, 2000 M Street NW, Suite 650, Washington, DC, USA, 200362014. 328 pages, 30.00 USD, Cloth.

Ducks, Geese, and Swans of North America – revised. By Guy Baldasarre. 2014. The Johns Hopkins University Press, 2715 North Charles Street, Baltimore, MD, USA, 21218-4363. 1,088 pages, 69.95 USD, Cloth.

Fishes: A Guide to Their Diversity. By Philip A. Hastings, H. J. Walker Jr., and Grantly R. Galland. 2015. University of California Press, California-Princeton Fulfillment Services, 1445 Lower Ferry Road, Ewing, NJ, USA, 08618. 336 pages, 65.00 USD, Cloth.

* **An Indomitable Beast: The Remarkable Journey of the Jaguar.** By Alan Rabinowitz. 2014. Island Press, 2000 M Street NW, Suite 650, Washington, DC, USA, 20036. 304 pages, 30.00 USD, Cloth.

Marmot Biology – Sociality, Individual Fitness, and Population Dynamics. By K. Armitage. 2014. Cambridge University Press, 32 Avenue of the Americas, New York, NY, USA, 10013-2473. 405 pages, 120.00 USD, Cloth.

The Passenger Pigeon. By Errol Fuller. 2014. Princeton University Press, 41 William Street, Princeton, NJ, USA, 08540-5237. 184 pages, 29.95 USD, Cloth.

Pilgrims of the Air. By John W. Foster. 2014. Notting Hill Editions, Widworthy Barton, Widworthy, Devon, UK, EX14 9JS. 240 pages, 25.00 USD, Cloth.

* **Penguins – The Ultimate Guide.** By Tui De Roy, Mark Jones, and Julie Cornthwaite. 2014. Princeton University Press, 41 William Street, Princeton, NJ, USA, 08540-5237. 240 pages, 35.00 USD, Cloth.

RSPB Seabirds. By Marianne Taylor. 2014. Bloomsbury Publishing PLC., 50 Bedford Square, London, UK, WC1B 3DP. 240 pages, 25.00 GBP, Cloth.

Woodpeckers of the World. By G. Gorman. 2014. Christopher Helm-Bloomsbury Publishing PLC., 50 Bedford Square, London, UK, WC1B 3DP. 528 pages, 35.00 GBP, Cloth.

BOTANY

Common Lichens of Northeastern North America – A Field Guide. By Troy McMullin, and Frances Anderson. 2014. Koeltz Scientific Books, P.O. Box 1360, D-61453 Koenigstein, Germany. 194 pages, 49.00 EUR or 63.70 USD, Paper.

* **Sedges of Maine: A Field Guide to Cyperaceae Paperback.** By Matt Arsenault, Glen H. Mittelhauser, Don Cameron, Sally C. Rooney, and Jill E. Weber. 2013. The University of Maine Press, 126A College Avenue, Orono, ME, USA, 04473. 712 pages, 29.50 USD, Paper.

OTHER

Experimental Evolution and the Nature of Biodiversity. By Rees Kassen. 2014. Roberts and Company Publishers, 4950 S. Yosemite Street, F2 #197, Greenwood Village, CO, USA, 80111. 288 pages, 36.00 USD, Paper.

The Analysis of Biological Data, Second Edition. By Michael Whitlock, and Dolph Schluter. 2014. Roberts and Company Publishers, 4950 S. Yosemite Street, F2 #197, Greenwood Village, CO, USA, 80111. 864 pages, 99.00 USD, Cloth.

* **Climber's Paradise – Making Canada's Mountain Parks, 1906–1974.** By Pearl A. Reichwein. 2014. University of Alberta Press, Ring House 2, Edmonton, AB, Canada, T6G 2E1. 432 pages, 45.00 CAD, Paper.

Conservation Science: Balancing the Needs of People and Nature, Second Edition. By Peter Kareiva, and Michelle Marvier. 2014. Roberts and Company Publishers, 4950 S. Yosemite Street, F2 #197, Greenwood Village, CO, USA, 80111. 672 pages, 72.00 USD, Paper.

A Field Guide to Economics for Conservationists. By Brendan Fisher, Robin Naidoo, and Taylor Ricketts. 2014. Roberts and Company Publishers, 4950 S. Yosemite Street, F2 #197, Greenwood Village, CO, USA, 80111. 208 pages, 36.00 USD, Paper.

* **Conrad Kain – Letters from a Wandering Mountain Guide, 1906–1933.** By Conrad Kain, and Zac Robinson *et al.* 2014. University of Alberta Press, Ring House 2, Edmonton, AB, Canada, T6G 2E1. 472 pages, 34.95 CAD, Paper.

* **Ian McTaggart-Cowan -The Legacy of a Pioneering Biologist, Educator and Conservationist.** Edited by Wayne Campbell, Dennis A. Demarchi, and Ronald D. Jakimchuck. Harbour Publishing, P.O. Box 219, Madeira Park, BC, Canada, V0N 2H0. 320 pages, 49.95 CAD, Cloth.

* **The Real Weed Man: Portrait of Canadian Botanist Gerald A. Mulligan.** By Julie M. Mulligan (author and publisher; available from Amazon.com). 2014. 228 pages, 19.99 USD, Paper, e-book 2.99 USD.

News and Comment

The Canadian Herpetologist (TCH) 4(2), Fall 2014

The Canadian Herpetologist (TCH) is a publication produced twice each year by the Canadian Association of Herpetologists and the Canadian Amphibian and Reptile Conservation Network.

CONTENTS: CHS Executive Members — Instructions for Authors — Editorial Notes —Meetings— Feature Articles: Unveiling of an Educational Panel Commemorating Over 40 Years of Turtle Research in Algonquin Provincial Park *by P. Moldowan, J. Litzgus and R. Brooks*; Nest Site Overwintering by Northern Map Turtle (*Graptemys geographica*) Hatchlings and Nest Site Protection at a Major Nesting Site in Quebec *by D. Fournier* — Field Notes: An Overview NCC's Conservation Efforts for Endangered Herpetofauna in the Ottawa Valley (Quebec) *by M. Saumur*; Calgary Zoo Centre for Conservation & Research 2014 Fieldwork Update *by L. Randall*; Fall Update on the Ojibway Massasauga Recovery Program *by J. Choquette*; First Northern Map Turtle (*Graptemys geographica*) Capture in Algonquin Provincial Park *by P. Moldowan*; Record Size Female Blanding's Turtle (*Emydoidea blandingi*) Found in Algonquin Provincial Park *by P. Moldowan*; Toad Tales from Long Point, Ontario (PART 1) *by K. Yagi*; Toad Tales from Long Point, Ontario (PART 2) *by F. Papini* — Thesis Abstracts in Canadian Herpetology: **Moldowan, P.D.** M.Sc. 2014. Laurentian University, Sudbury, Ontario. (Supervisor: J.D. Litzgus). Sexual dimorphism and alternative reproductive tactics in the Midland Painted Turtle (*Chrysemys picta marginata*) — **Crosby, J.** MES. 2014. University of Waterloo, Waterloo, Ontario. (Supervisors: S. Murphy and S. Ashpole). Amphibian occurrence on south Okanagan roadways (2010-2012): Investigating movement patterns, crossing hotspots and roadkill mitigation structure use at the landscape scales. — Recent Publications in Canadian Herpetology — News and Announcements — CHS/SHC Membership Form.

Upcoming Meetings and Workshops

Northeast Natural History Conference 2015

The 15th Northeast Natural History Conference (NENHC) hosted by The Association of Northeastern Biologists to be held 18–20 April 2015 at the Sheraton Springfield Hotel in Springfield, MA. This is a 3 day conference which promises again to be the largest forum for researchers, natural resource managers, students, and naturalists to present current information on the varied aspects of applied field biology (freshwater, marine, and terrestrial) and natural history for the Northeastern United States and adjacent Canada. Registration is currently open. More information is available at http://www.eaglehill.us/NENHC_2015/NENHC2015.shtml.

Annual Conference of the Animal Behavior Society 2015

The 52nd Annual Conference of the Animal Behavior Society to be held 10–14 June 2015 in Anchorage, Alaska. More information is available at http://abs2015.org/.

International Conference on Biodiversity 2015

The 4th International Conference on Biodiversity to be held 15–17 June 2015 in Las Vegas, USA. The theme: "Share and Enhance Ecological & Geological Conservation research". Registration is currently open. More information is available at http://biodiversity.conferenceseries.com/index.php.

William Beverly Scott 1917–2014

An outstanding Canadian ichthyologist died 18 August 2014. William Beverly Scott (Bev) was born 7 July 1917 and raised in Toronto. After serving in the Canadian army in Europe in WWII he obtained his PhD at the University of Toronto in 1950 and was appointed Curator of Fishes at the Royal Ontario Museum with a cross-appointment to the Department of Zoology, University of Toronto. In 1950-1976 he built the research fish collection at the ROM to be the largest in Canada and it has continued to grow under E. J. Crossman, A. Emery, R. Winterbottom and H. López-Fernández. It now contains 97,600 cataloged lots containing a little over 1,127,636 specimens representing 6,677 valid species in 415 families (Erling Holm: 27 November 2014). For contrast, the next largest Canadian collection is held by the Canadian Museum of Nature has 60, 828 catalogued lots for a total of 679,522 specimens representing 4,025 species (Sylvie Laframboise: 28 November 2014).

In 1976, Bev moved to St. Andrews, New Brunswick, where he became Director of the Huntsman Marine Science Centre, a laboratory run by a consortium of Canadian Universities. There he established the Atlantic Reference Center, one of North America's largest collections of larval fishes. After Bev's retirement from the Huntsman in 1982, he served as a Huntsman Senior Scientist, even after moving to Kingston, Ontario in 1998.

While with the ROM, Bev coauthored *Freshwater Fish of Canada* (1973) with E. J. Crossman (Ed) who had come to the ROM in 1957 after obtaining a MSc from the University of Toronto and a PhD from the University of British Columbia. Ed succeeded Bev as Curator of Fishes. He died in December 2004 and an often discussed revision never materialized. Still at the ROM, Bev completed a monograph *Fishes of the Atlantic Coast of Canada* (1966) started earlier by A. H. Leim, but left unfinished at his death. Subsequently at Huntsman, as more information accumulated for the region, a completely new volume was undertaken by Bev with his wife, Milly, as coauthor: *Atlantic Fishes of Canada* (1988). Bev and Milly moved to Kingston when Milly's health deteriorated and she died there in 2006. Bev subsequently moved to Lindsay, Ontario, where both his children live, but remained in contact with colleagues at the ROM and elsewhere.

Bev frequently served *The Canadian Field-Naturalist*, as he did for other scientific journals, as a reviewer of ichthyology papers. His last contribution was a review of a book by longtime ROM colleague Glenn B. Wiggins: *Biological Notes on an Old Farm: Exploring Common Things in the Kingdoms of Life*. Canadian Field-Naturalist 123(4): 387.

Appreciation for contributions and corrections to an earlier draft are due (by institution) Erling Holm, Rick Winterbottom, Ross MacCulloch (Royal Ontario Museum) Sylvie Laframboise, Brian Coad (Canadian Museum of Nature), C. G. Gruchy (retired, formerly Canadian Museum of Nature), and Lou Van Guelpen (Curator of Fishes and Collections manager, Atlantic Reference Centre The Huntsman Marine Science Centre). Also consulted was the tribute based on an interview by David G. Smith.:*William Beverly Scott* Copeia 2006: 307–315, and a DFO Science and Research feature on-line article: *Not the Retiring Kind: Scientist emeritus Bev Scott.*

FRANCIS R. COOK

The Ottawa Field-Naturalists' Club Awards for 2013, presented April 2014

ELEANOR ZURBRIGG, IRWIN BRODO, JULIA CIPRIANI, CHRISTINE HANRAHAN, AND ANN MACKENZIE

On April 26th, 2014 members and friends of the Ottawa Field-Naturalists' Club gathered for the Club's Awards Night at St. Basil's Church in Ottawa to celebrate the presentation of awards for achievements in the previous year. Awards are given to members or non-members who have distinguished themselves by accomplishments in the field of natural history and conservation or by extraordinary activity within the Club. Three awards were presented for 2013, recognizing achievement in enhancing the profile of the Club, long time service as editor for one of the Club's publications, and success in raising awareness of environmental stewardship and respect for nature in the primary school program.

Member of the Year: Mark Brenchley

The OFNC's Member of the Year award recognizes the member judged to have contributed the most to the Club in the previous year.

We are recognizing Mark Brenchley for his positive, creative and enthusiastic commitment. Mark Brenchley joined the OFNC in 2012 upon his return to Ottawa. In late 2012 and throughout 2013 he jumped in to support the Education and Publicity Committee. His energy, skills and ideas were pivotal to the completion of several projects designed to enhance the profile of the Club.

When Ontario Nature invited naturalist clubs to sponsor a youth to attend the Ontario Nature Youth Summit last year, the request landed in the hands of the Education and Publicity Committee. Mark stepped up to design an application process to select a candidate to represent the Club. He communicated with school boards, scouting groups and the members of the Club to generate interest in the opportunity. Three applications came back to him. Mark, Suzanne Deschênes and Lynn Ovenden interviewed the candidates and selected Sarah Wray, a grade 10 student at Nepean High School. After the Summit, Mark invited Sarah to describe her experience at a monthly meeting in the Fall and asked her to write a report which was published in the 2014 Winter issue of *Trail and Landscape*.

Had Mark not taken the Ontario Nature initiative, the club would have missed an opportunity to support the Summit and Sarah. Thanks to his initiative, there is a framework in place to support the Club's future participation.

Over the year, Mark worked on a series of promotional items and signs, all bearing the OFNC's owl logo, the club name and often the website on a forest green background. He made an 8' long banner that tops our tent and display table at public events. When Education and Publicity wanted to offer hand lenses on a club lanyard at the monthly meeting sales table, Mark created the logo file and placed the order with the lanyard imprinting company. Then he coordinated the logo design and purchase of the lens wipe pouches which clip onto a lanyard or binocular strap. He led the design of a promotional bookmark which includes photos and the Club website.

The OFNC Council realized a few years ago that the sign at the entrance to Fletcher Wildlife Garden is a highly visible spot, a great place to increase public awareness of OFNC. Although there has been a sign on Prince of Wales Drive to direct people to the Garden, there was nothing to indicate the OFNC's involvement with the Garden. Since Mark is in the sign business, he was asked what could be done. As a result he designed and installed a dark green aluminum panel with the OFNC owl and our website atop the existing Fletcher sign clearly identifying the Fletcher Wildlife Garden with the OFNC, all at minimal cost to the Club.

Through these products Mark has developed several graphic files with the OFNC's logo and wordmark. He continues to work at "branding" the OFNC with the goal to create a recognizable visual identity for all Club-related materials, promotional items and signage.

Mark is a cheerful, engaging salesman behind the display table at most monthly meetings and at some of OFNC's public events. It is for his many contributions to promoting the Club in 2013 that we want to recognize Mark as Member of the Year.

(Written by Julia Cipriani based on information and feedback from Lynn Ovenden)

George McGee Service Award: Karen McLachlan Hamilton

The OFNC George McGee Service Award is given in recognition of a member who has contributed significantly to the smooth running of the Club over several years.

This year, the award goes to Karen McLachlan Hamilton, long-serving editor of *Trail & Landscape*. All club members are familiar with our quarterly publication, more commonly known as *T&L*, in which news of the club, regional biological and conservation reports and articles by members, lists of upcoming events, poems, photos and much else is published. Every three months, this lively and informative publication arrives

in our mailboxes, to be enjoyed and savoured. I would guess, however, that many of us give little thought to the work and effort that ensures *T&L* lands in our laps four times a year!

From its inception in 1967, when it was produced five times a year, to today's much more substantial quarterly, *Trail & Landscape* has had only 6 editors, as each tends to stay for a long time. Karen McLachlan Hamilton has served in that capacity since 2001 and has overseen the production of more issues (52 to the end of 2013) than anyone since founding editor Anne Hanes (65 issues).

Karen is responsible for seeking articles, editing them for technical accuracy and presentation, providing feedback and suggestions to authors, and making sure the publication is ready for the printer. In this, she is helped by an associate editor, a production coordinator and a mailing team. But the ultimate responsibility for ensuring the quality and production standards of *T&L* (presentation and timing etc.), is Karen's. No sooner has she put one issue "to bed", than she is working on the next, for there is little downtime in this business. It is astonishing that Karen, with a full-time job, is able to maintain this hectic schedule with professionalism and grace. While an honorarium goes along with the position of Editor, it does not begin to compensate for the actual work and time that goes into this process. And besides, Karen has always refused to accept the stipend. It is indeed, a labour of love.

Karen not only edits *T&L*, she also writes many articles for it, such as the annual summary of the OFNC's Soiree and Awards Ceremony. She has also written numerous book reviews for *T&L*, which are characterized by a forthright discussion of the books in question, incisive comments on content, and descriptive information on the books themselves. Karen is also a long-serving member of the OFNC Board of Directors and the club's Publications Committee.

For all these reasons, we believe that Karen is very well deserving of this award to recognize her long service on behalf of the OFNC.

(*Written by Christine Hanrahan*)

Mary Stuart Education Award: Angelika Skevington

The Mary Stuart Education Award is given in recognition of outstanding achievements in the field of natural history education in the Ottawa Region.

Angela Skevington is the recipient of this award for 2013. Angela is a primary school teacher who is passionate about natural history education. For over 15 years she has taught a variety of grades in different schools, sharing her dedication to good environmental stewardship and her knowledge and wonder of nature with her students every day, every year. Currently Angela teaches a combined Grade 4/5 class at Huntley Centennial Public School in the village of Carp near Ottawa.

Wherever she works, Angela has championed such environmental programs as EarthCare Canada and more recently Ontario EcoSchools. Last year her school was recognized with a silver level EcoSchool certification. This achievement required years of diligent effort on Angela's part to engage students and the school community in activities across the 6 areas of environmental practice rated by the EcoSchool Program, including waste minimization and energy conservation. Each school year, she instigates a student-led club (previously called an EarthCare Club, currently dubbed *The Dragonflies*) that undertakes environmental projects, such as a periodic audit of their school's energy and waste practices. If the audit indicates that there is a problem, such as improper waste disposal, then *The Dragonflies* club delivers classroom presentations to fellow students demonstrating the proper practice, such as how to separate garbage for recycling. The students in *The Dragonflies* club also put on plays at school assemblies to demonstrate proper energy and waste practices. Last year, Angela piloted "litterless lunches" with her class. *The Dragonflies* promoted the idea and this year the whole school is litter-free at lunch. There are many more examples. Through this hands-on practice, students learn how to be active environmental stewards.

For the past 3 years, Angela has participated in Ottawa's Clean up the Capital Day. She enlisted classes that were interested in being involved, applied through the City of Ottawa to get materials (bags, gloves) and then they cleaned up the school grounds.

On Earth Day, Angela has conducted student plays at the school assemblies featuring pollution, anti-littering, proper recycling. She also encourages the students to create and perform skits, songs and presentations. She does this every year to promote celebration of the natural environment and good environmental stewardship.

Field trips and nature appreciation are important parts of Angela's teaching. Habitat is part of the Grade 4 curriculum. She has successfully applied through Ducks Unlimited Canada's Project Webfoot for funding for field trips to a local wetland (such as the Bill Mason Outdoor Education Centre). They have also had field trips to the Bonnechere Caves.

In addition to all of this, Angela leads informal lunchtime field trips for interested students to a nearby natural area, to learn about and develop an appreciation for nature. One day they may focus on birds, the next day on insects, and the third on plants. She applied for and received funding to organize a field trip for *The Dragonflies* club for a day to learn about bird banding at Innis Point Bird Observatory. The children were excit-

ed to each hold a chickadee or nuthatch. On breaks they played nature games in the field, and went on a nature hike.

Angela teams up with her husband Jeff Skevington to help him lead "kid friendly" field trips for The Ottawa Field-Naturalists' Club as well as for other nature clubs in the Ottawa Valley. Angela assisted Jeff and colleagues in hosting a well-attended Bug Day held at the Fletcher Wildlife Garden last year.

Angela's efforts are recognized and appreciated, as evidenced by fellow teacher Donna Christie who said: "I feel honoured to work with Angela and know that she has made a positive impact on her students and our school .... She is a scientifically-oriented, dedicated, hard-working educator."

The OFNC is delighted to present the Mary Stuart Education Award for 2013 to Angela in recognition of her success in raising awareness of environmental stewardship and respect for nature at her school and more broadly.

(Prepared by Eleanor Zurbrigg with input from Donna Christie)

Index to Volume 128

Compiled by William Halliday

Note: Page references are to the first page of the item (e.g., article, note), and as such are not always to the exact word location.

Index to Book Reviews

Book Reviews

News and Comment

Club Awards

Index to The Canadian Field-Naturalist Volume 128

Mailing date of the previous issue 128(3): 20 October 2014

THE CANADIAN FIELD-NATURALIST Volume 128, Number 4 2014

Articles

(continued on inside back cover)

ISSN 0008-3550